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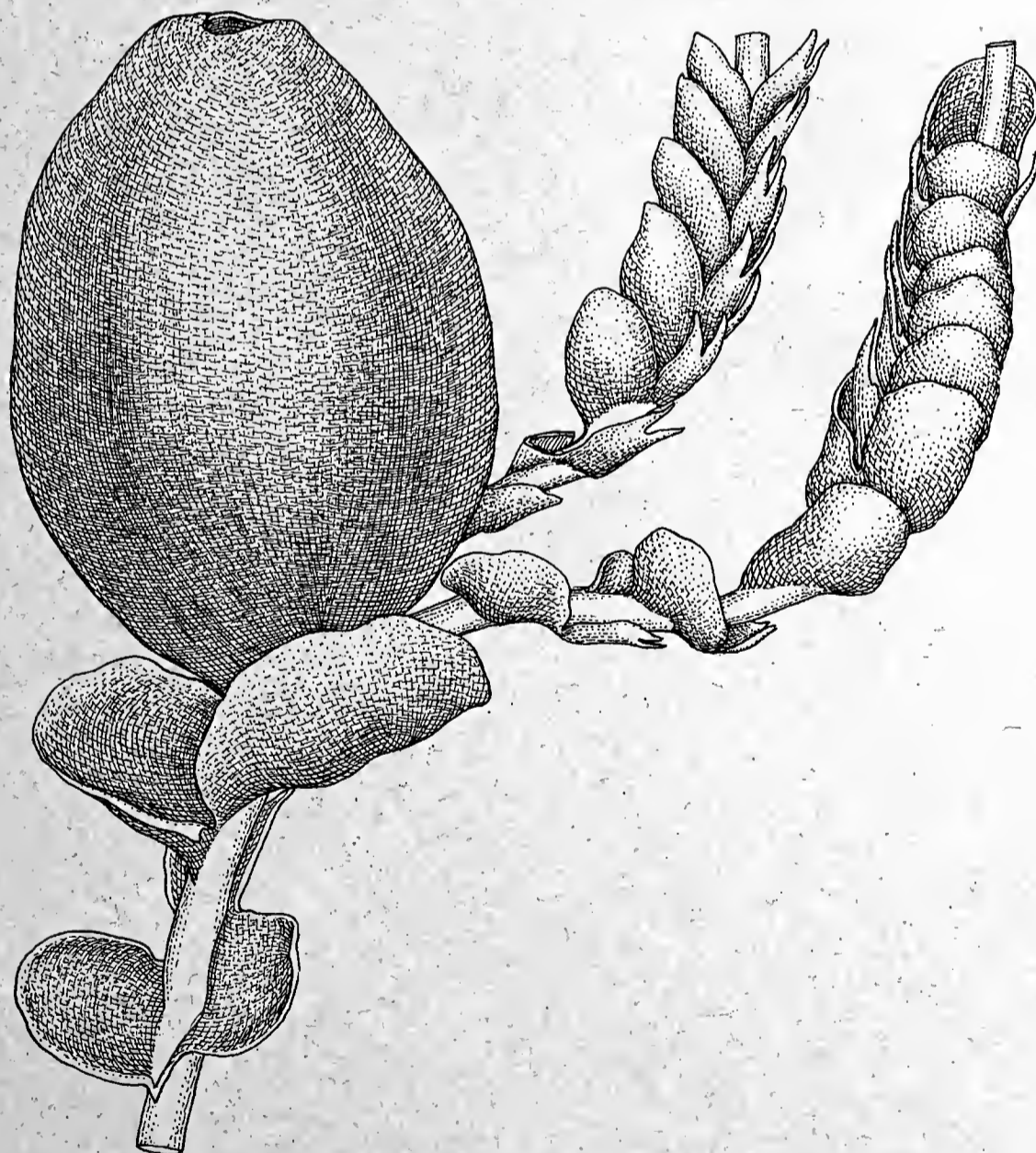
Botany

NEW SERIES, NO. 47

**In celebration of Dr. John J. Engel:
A tribute to 40 years in Bryology**

**Editors,
Matt von Konrat
Sabine Huhndorf**

*Department of Botany
The Field Museum,
1400 South Lake Shore Drive
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**Accepted May 20, 2008
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PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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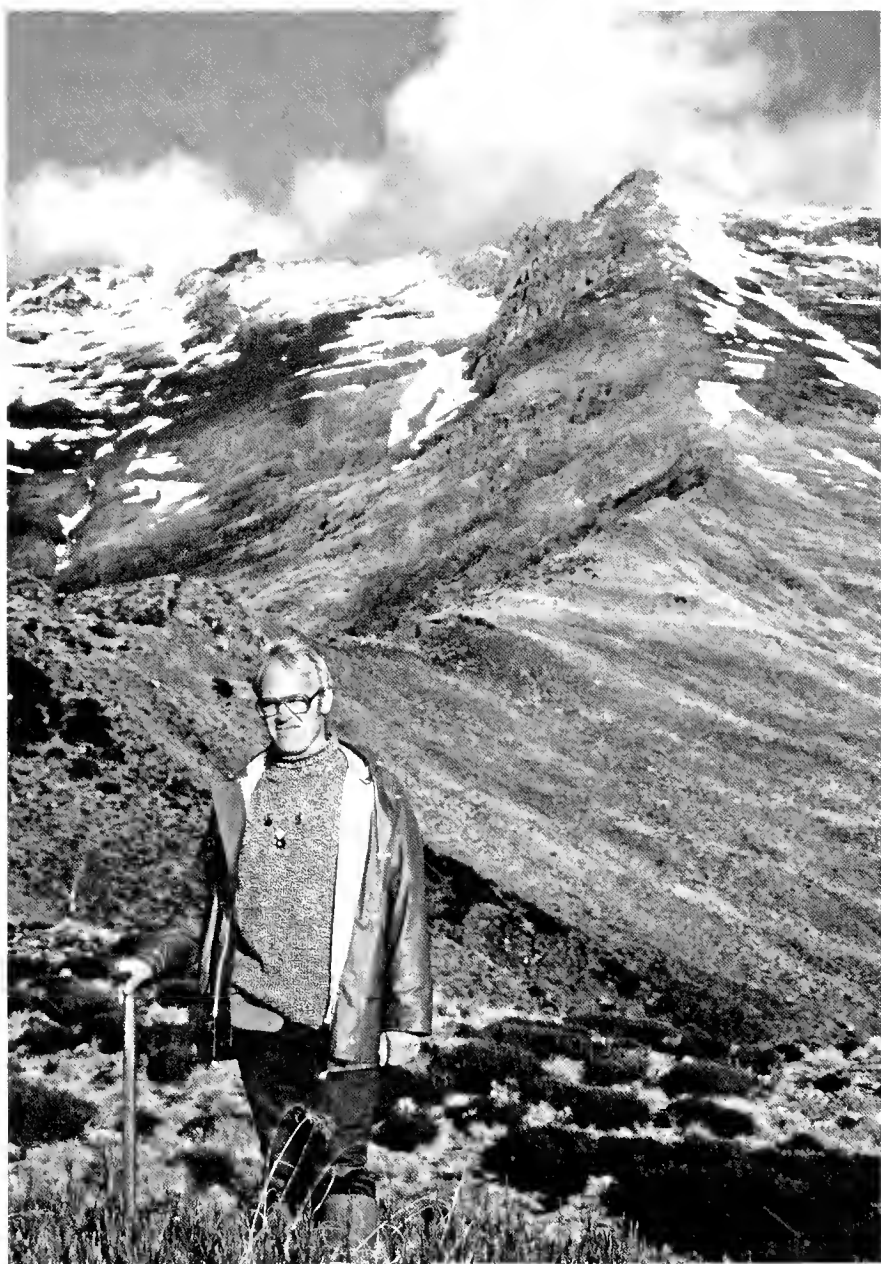
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Foreword

The concept of a Festschrift volume in celebration of the illustrious career of Dr. John Jay Engel was conceived, at the time of writing, almost 18 months ago. Yet the concept was made into a reality with the generous financial support from both *Fieldiana* and the office of the head of collections and research, Dr. Lance Grande. When we began planning for the Festschrift, we were far removed from the reality of such a project—although we had been strongly warned by our colleagues that such a venture would be a major undertaking! The success of the project can be attributed to a community effort and is owed to all those who participated as reviewers, contributors, and editorial support.

The Festschrift, in celebration of over 40 years in the field of bryology by Dr. Engel, provides a rare opportunity to have in a single volume a collection of publications solely dedicated to liverworts and hornworts. We begin the Festschrift with special acknowledgments and a list of the contributors themselves. This is followed by part 1, which includes a brief biography of Dr. John J. Engel himself; a tribute by friend and colleague, Dr. John E. Braggins; and a letter from his wife and two daughters.

In preparing for the volume, it appears that the study of liverworts and hornworts remains strong, as it was an encouraging sign to receive contributions from senior scientists, postdocs, researchers, and senior Ph.D. students. There are 18 scientific papers by 34 authors and three biographic articles as well as a full bibliography of John Engel's publications. The overall quality of the articles in this volume is outstanding, and we hope the broad scope of papers will draw wide appeal and interest. The papers cover a broad array of disciplines, including chemistry, anatomy, cytology, life

history, and physiology. The taxonomic studies are particularly encouraging, with researchers utilizing large sets of tools at their disposal in order to unravel species relationships, including phylogenetic reconstructions based on molecular data and morphometric analysis.

The Festschrift is divided into nine parts. Following the first part of the biographic articles, the 18 scientific papers are divided into eight parts. Despite the breadth of papers, there is a major focus on liverworts and hornworts of the Southern Hemisphere; however, Northern Hemisphere elements are also included. The geographical emphasis, of course, reflects Dr. Engel's active research programs, particularly of southern South America and Australasia. Part Two investigates the life cycles of bryophytes and emphasizes the critical position of liverworts and hornworts in the study of early land plant evolution. Part Three includes a paper each on chemistry and physiology. Part Four also includes two papers, one on patterns of leaf development and one on chromosome studies. Part Five, comprised of two papers, continues an exciting project that analyzes floristic and diversity patterns using global-scale data sets—a project that involves Dr. Engel himself as a collaborator. The eight taxonomic and floristic studies, which include descriptions of new species and a new genus, are divided into two parts based on geography: Part Six includes five papers with a geographical focus on Asia and Australasia, and Part Seven includes three papers with a geographical focus on North and South America. Part Eight includes two papers on hornworts, and, finally, Part Nine concludes the Festschrift with a single paper on etymology of genera from Australia.

Matt von Konrat and Sabine Huhndorf

Acknowledgments

We were delighted by the enthusiastic response from all the contributors who kindly accepted our invitation to submit manuscripts and the reviewers who agreed to provide scientific appraisal. We extend our thanks to all of them as well as editorial support, which together made the *Festschrift* a great success.

Over 40 people, including both authors and reviewers representing 14 countries, contributed to the scientific content. We wish to provide special gratitude to all the reviewers. These include Prof. Dr. Alicia Bardon (Tucumán National University, Tucumán, Argentina), John Braggins (Auckland War Memorial Museum, Auckland, New Zealand), Mary Berbee (University of British Columbia, Vancouver, BC, Canada), Elizabeth A. Brown (Royal Botanic Gardens, Sydney, Australia), D. Christine Cargill (Australian National Herbarium, Canberra, Australia), Barbara J. Crandall-Stotler (Southern Illinois University, Carbondale, IL, U.S.A.), Christine Davis (Duke University, Durham, NC, U.S.A.), Paul Datson (Hort Research, Auckland, New Zealand), Paul G. Davison (University of North Alabama, Florence, AL, U.S.A.), David Glenney (Landcare Research, Lincoln, New Zealand), Bernard Goffinet (University of Connecticut, Storrs, CT, U.S.A.), Robbert Gradstein (University of Göttingen, Göttingen, Germany), Xiaolan He-Nygrén (University of Helsinki, Helsinki, Finland), Jochen Heinrichs (Georg August University, Göttingen, Germany), Jaakko Hyvönen (University of Helsinki, Helsinki, Finland), David Long (Royal Botanic Garden, Edinburgh, Scotland, U.K.), David Meagher (The University of Melbourne, Melbourne, Australia), Dan Nicolson (Museum of Natural

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Even though we have felt solely burdened at times, it was only a delusion. We have had invaluable support. Anders Hagborg (research assistant, The Field Museum), who was a volunteer at the time, meticulously went through the manuscripts and assisted in checking references, style, and format and identified typographical errors. Laura Briscoe, who is a recent addition to the bryology program, soon got indoctrinated and assisted with editing and reproduction of plates. We are also very grateful to the support offered by Harold Voris, managing scientific editor of *Fieldiana* and his support staff as well as the copy editors at Allen Press. We are also appreciative of the valuable contributions of Dr. John E. Braggins and John Engel's wife, Karen Engel, and his two daughters, Beth and Laura Engel. We are indebted to the support of the chair of Botany, Michael Dillon, for his support from the outset. Finally, the *Festschrift* was made into a reality with the generous financial support from both *Fieldiana* and the office of the head of collections and research, Dr. Lance Grande.

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Introduction

If you ever have the opportunity to do fieldwork with Dr. John Engel in New Zealand, it will not be long until John, with great delight, will tell you about his fond memories of what he recalls as the “glory years” back in the early 1980s. John, of course, has many stories of his experiences spanning his career. Here, I briefly outline John’s professional career but leave some early recollections to his family and Dr. John Braggins, his friend and colleague of almost two decades, who also provides a brief commentary of his academic career.

John Jay Engel was born July 27, 1941, in Milwaukee, Wisconsin; has been married to Karen Engel for 45 years; and has two daughters, Beth and Laura Engel. By 1965, John had obtained his B.S. and M.S. from the University of Wisconsin, Milwaukee. From 1967 to 1972, he

undertook his Ph.D., which was followed in the same year as a postdoctoral research associate, both at Michigan State University. John himself acknowledges his “special heartfelt thanks” to Dr. Henry Imshaug for his interest and invaluable guidance throughout John’s years at Michigan State. This foundation at the University of Wisconsin and Michigan State University was to set the scene for a distinguished and still thriving career some 40 years later.

In reviewing a career spanning over 40 years, including over 35 years at the Field Museum, the number of professional appointments, grants, and awards run the length of one’s arm. The following is a brief synopsis of that career. After a position as a Michigan State University, John took up the position as Donald Richards Assistant Curator of Bryology at the Field Museum. In 1977, John was promoted to associate curator, followed by curator in 1986. John Engel also

served as acting chairman of the Department of Botany from September 1987 to May 1988, followed by a term as chairman from June 1988 to September 1993.

Service to the Field Museum and Scientific Community

As I contemplate John's professional career, accomplishments, and service at the Museum after perusing his *curriculum vitae* and talking to his colleagues, I am aware of the variety of responsibilities he has assumed during his career, some because he was obligated, some because of circumstances, and some because they interested him. As a staff member of the Museum and involved in several committees myself, the number of committees that are active and historical was almost bewildering. John must have served on almost all of them! Some are prominent and others less so. A selection of committees John has served on include Space Planning Committee (several occasions through years); chairman, Ad Hoc Curatorial Search Committee (several occasions through years); member, Science Advisory Council, 1977–1987, 1997–2003; chairman, Science Advisory Council, 1980–1981; supervisor, Scientific Illustrators, 1982–1995; member, Scholarship Committee, 1985–1986; member, Committee for Visiting Scientist Program, 1985–1986; chairman, Publications Committee, 1987–present; vice president, Selection Committee, 1988–1989; Collections Committee, Strategic Planning Process, 1992; member, Centennial “Art in Motion” project committee, 1992–1993; and codeveloper, “Where Science and Education Meet: Finding Cures for AIDS from Plants,” 1992.

John is also an active participant in the scientific community outside the Museum in several capacities. John is a curatorial affiliate in the Division of Botany, Peabody Museum of Natural History, Yale, as well as serving on the editorial board for the journal *Nova Hedwigia* (Germany) and for the *Index Hepaticarum Supplementum* series.

Grants and Awards

John Engel has obtained various grants and awards throughout his career. A significant

number of these supported an extensive field program that has contributed to the success of his research. A vast majority of grants were awarded by the National Geographic Society, with three of these obtained in the past five years alone: 2003, 2006, and 2007. John has also received grants from the National Science Foundation (NSF). The most prominent was awarded in 2006 as part NSF's Assembling Tree of Life program titled “Assembling the Liverwort Tree of Life: A Window into the Evolution and Diversification of Early Land Plants.” The project runs until 2010 and involves collaborative research between five institutions, led by Dr. Jon Shaw of Duke University, who is the principal investigator, the Field Museum, Southern Illinois University, and the University of Connecticut.

Foreign Fieldwork

From the outset of John Engel's career, he has had an extensive field career that has provided him great insight into the ecology and habit of liverworts. This has also afforded him the opportunity to study live plants and therefore critical characters such as oil bodies that are not available from dried herbarium material alone. John's first foreign expedition, as part of his M.S., was to the Juan Fernandez Islands in 1965 organized by Raymond Hatcher. This was followed by expeditions to the Falkland Islands in 1967 and 1968 and five times to southern Chile, including 1967–1968, 1969, 1976, 2004 (Tierra del Fuego), and 2005 (Tierra del Fuego). John Engel has also collected from the remote Kerguelen Islands of the South Indian Ocean in 1971. In 1973 and 1975, John collected liverworts from Costa Rica. John Engel's first excursion to Australasia was in 1971 with a brief trip to New Zealand. Since this time, John has done fieldwork in Tasmania in 1976–1977 and 1982–1983 and mainland Australia in 1976–1977. John has since developed a very strong and active field program in New Zealand, having been there seven times, including 1971, 1982–1983, 1995, 1997, 2003, 2006, and, most recently, 2007. Fieldwork has extended into the northern hemisphere in Spain in 2000 and 2001.

I myself first met John in 1996 in the capacity as a Ph.D. student, and we shared funds for what was both our first helicopter trip. Since that time, we have been together in the field on three separate occasions. Obviously, after much time in

the field and as colleagues, there are dozens of anecdotal stories. Some of these “stay in the field.” However, an anecdote that I believe will stay in my mind for some time to come was from our most recent field trip to New Zealand in 2007. For a short time, John Engel was considered a fugitive from the law! We had just returned from the field, when John Braggins had left us a message on our cell phone informing John he needed to report to the nearest police station, as he was purportedly wanted for a hit-and-run accident. Apparently, they were placing a stop on his passport and were going to contact INTERPOL. Of course, the witness had misidentified the car registration number. John had to report to a police station to prove we were actually in a helicopter at the time, hundreds of miles from where the accident had taken place.

Significant Scientific Contributions

Noteworthy is John Engel’s commitment to both collections and research. Significant growth of the bryophyte collection at the Field Museum has occurred through John’s active research and field programs over the past three and half decades. John has collected over 20,000 liverwort specimens, representing an invaluable resource and in many cases the only collections from an area. Thus, John Engel’s continuing floristic and monographic research on austral hepatics has made the Field Museum one of the centers for studies of this group.

Throughout John’s tenure at the Field Museum, he has actively encouraged researchers and collectors to deposit their material at the Museum. Through gift and exchange and occasionally through purchase, John Engel has overseen the acquisition of some critical collections that have helped solidify the Field Museum as a center of study for liverworts, especially those from the austral region. The most significant component of the bryophyte collection is the purchased hepatic herbarium of R. M. Schuster, which is equal in worldwide geographical coverage, systematic breadth, and nomenclatural importance to the major 19th-century hepatic collections of Stephani (G) and Schiffner (FH). The herbarium (ca. 58,000 specimens) is being transferred to the Field Museum in stages. Several other important collections acquired through gift and exchange under John’s tenure includes R. E. Hatcher (Chile

and New Zealand), J. Child (New Zealand), M. Lewis (Alaska, Bolivia), H. Roivainen (southern South America), and R. Ochyra (Antarctica).

Far from retirement, John has had a very full and productive 40 years, which is exemplified by the over 115 papers he has published, with some of them book length in nature, in over 20 journals. John Engel has described or coauthored 14 new genera and over 130 new species and infraspecific taxa of liverworts. In addition, the taxonomic activity of John’s work can be measured by the more than 370 taxa that have been taxonomically reassigned. Perhaps illustrating John Engel at the peak of his career, at the time of writing, is the first of a projected three-volume set on the liverworts and hornworts of New Zealand, which represents the first flora for this group of plants in the southern hemisphere. This promises to be an outstanding treatise. John has also had a number of liverwort species named after him in his honor, including a few more in this volume!

On a personal note, I have been greatly enriched by my interactions with John both at the Field and in the field and by the knowledge he shares and communicates. When one spends six to eight weeks at a time working long enduring hours, often under stressful situations, a sense of humor, patience, and understanding greatly helps. John



FIG. 1. Dr. John J. Engel in the field in Aotearoa/New Zealand. Dr. Engel is a meticulous note taker in the field.



FIG. 2. Dr. John J. Engel at Raetea State Forest, Northland, Aotearoa/New Zealand.



FIG. 3. Dr. John J. Engel accompanied with a helicopter pilot near Mt. Owen, Kahurangi National Park, Aotearoa/New Zealand.

has all these qualities. I hope he is content with this brief recollection and reflection on his accomplishments. The following is a (hopefully complete) list of John's publications in chronological order beginning in 1968 extending to the present date of writing, March 2008.

Publications on Bryology by John J. Engel

- ENGEL, J. J. 1968. A taxonomic monograph of the genus *Balantiopsis* (Hepaticae). *Nova Hedwigia*, **16**: 83–130, plates 27 (1)–59 (33).
- ENGEL, J. J., AND R. GROLLE. 1971. *Marsupidium* in South America. *Journal of the Hattori Botanical Laboratory*, **34**: 437–444, plates 1–2.
- ENGEL, J. J. 1972. The genus *Andrewsianthus* in South America and the Falkland Islands. *Bryologist*, **75**: 325–334, figs. 1–64.
- . 1972 [1973]. *Chiloscyphus hookeri* n. sp. and nomenclatural changes in the genus *Clasmatocolea*. *Journal of the Hattori Botanical Laboratory*, **36**: 150–156, plates 1–2.
- . 1973. On the typification of *Austrolophozia fuegiensis* (Steph.) Schust. *Journal of the Hattori Botanical Laboratory*, **37**: 181–183, 1 table.
- ENGEL, J. J., AND Y. KUWAHARA. 1973. *Metzgeria litoralis* sp. nov. and *Apometzgeria* from southern South America. *Bryologist*, **76**: 293–296, figs. 1–9.
- ENGEL, J. J., AND R. M. SCHUSTER. 1973. On some tidal zone Hepaticae from South Chile, with comments on marine dispersal. *Bulletin of the Torrey Botanical Club*, **100**: 29–35, 1 table.
- ENGEL, J. J. 1974. The Raymond E. Hatcher collection of Hepaticae and Anthocerotae from southern South America, with new taxa and notes on range extensions. *Bryologist*, **76**: 528–535, figs. 1–18.
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- ENGEL, J. J. 1975. Hepaticae and Anthocerotae collected by Dr. Harold E. Moore, Jr. in New Caledonia, Seychelles, Mauritius and Reunion in 1972. *Bryologist*, **78**: 361–362.
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- . 1975. Austral Hepaticae, V. Studies on Schistochilaceae. *Phytologia*, **30**: 241–250.
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- ENGEL, J. J. 1976. On the typification of *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle (Hepaticae). *Misc. Bryol. Lichenol. Miscellanea Bryologica et Lichenologica*, **7**: 75.
- . 1976. *Metzgeria hamata* Lindb., an illegitimate name of Hepaticae. *Lindbergia*, **3**: 219–220, fig. 1.
- . 1976. The southern South American Hepaticae and Anthocerotae collected by H. Roivainen in 1969–1970, with new taxa and notes on range extensions. *Annales Botanici Fennici*, **13**: 132–136.
- . 1976. Austral Hepaticae VI. Some new species and new combinations of taxa from southern Chile. *Bryologist*, **79**: 514–515.
- . 1977. Austral Hepaticae IX. *Anastrophyllum tristanianum*, a new species from Tristan de Cunha. *Fieldiana: Botany*, **38**: 71–74, figs. 1–2.
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- . 1978. A taxonomic and phytogeographic study of Brunswick Peninsula (Strait of Magellan) Hepaticae and Anthocerotae. *Fieldiana: Botany*, **41**: i–viii, 1–319.
- . 1979. Austral Hepaticae XI. Lophocoleaceae: New taxa, new combinations and re-alignments. *Phytologia*, **41**: 309–312.
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In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part One: Biographical Contributions

Chapter Two: A Letter from Down Under John E. Braggins

Herbarium, Auckland War Memorial Museum, Private Bag 92018, Auckland 1, New Zealand

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I met John in 1990. We had tried to get together earlier, but on that occasion I found when I got to the United States that he was in New Zealand and Tasmania. We soon found that we had a driving interest in liverworts and that my interest in close-up photography fitted in well with his drawing-based approach. He has had the advantage of a great herbarium collection and library at his fingertips, and this shows in the quality of his published work. It sometimes comes with the added complication of leading the department and the administrative duties associated with that, and we can be grateful that John survived those years to go on to his best work once he was free of those particular responsibilities.

John is wonderfully fit and capable in the field; he is an enthusiastic cyclist at home, though on one visit he did eventually learn that I am essentially incompetent on two-wheeled machinery. His enthusiasm in the field has led to a need to round him up when the day or the weather

runs out; it is rare indeed that he is the one wanting to stop collecting and head for home, transport, and so on. This is of course a quirk shared by many bryophytic colleagues and the bane of those organizing trips with more than one stop.

John is an excellent host and can make even a winter visit to a frozen city a pleasure to undertake. His understanding of the weather conditions in his home city and the reality of inadequate clothing possessed by visitors from much more temperate and benign climates made for a successful time even though two heavy snowfalls within a month were way beyond my limited experience and not something I am in any hurry to repeat. Chicago in autumn as experienced on an earlier visit is a much more acceptable climate. John's enthusiasm for his tomato crop that time was exceeded only by his dog's enthusiasm in helping demolish the crop, not something I ever dreamed a dog would be enthusiastic about. John,

however, was quite happy to share his crop with his four-footed mate.

John has a remarkable ability to explain what a particular plant is in the field and how he differentiates it from other similar species. This was particularly apparent on a trip on Mt. Owen, where a range of *Chiloscyphus* species were encountered. John was able to also here demonstrate his fitness with a much heavier pack and the ability to keep going longer than anyone else. His excitement in discovering the range of species in sinkholes in this area was wonderful to witness.

John holds firm opinions on the use of words and descriptions, and the long train commute to and from work has provided a great opportunity to air and discuss such differences. It is always with a great sense of achievement if any revision of his description has taken place, and also at that point you are sure you have really explained fully why a particular view should predominate. He does not easily concede the value of different viewpoints but can be convinced by good reasoning.

John rightly regards his collections as precious records and takes great care of them in the initial drying stage. I have memories of motel rooms with little floor space left apart from the serried

ranks of drying packets. John would always make the extra effort to find better spots for them to dry, and with our fickle weather they sometimes had to be rescued in haste. None of this ever seemed to faze him.

His care of specimens is matched by his meticulous attention to the history of the names of the species reflected in the detailed synonymy that features in many of his papers. The frustration associated with losing a familiar name is rewarded by a new and more stable platform for the future, as long as our failing memories can cope with a range of new names. This is a skill in integrating the range of older literature and again reflects his familiarity with the library holdings at the Field Museum.

As well as its botanical resources, John has an excellent knowledge of many aspects of his Museum. Suggestions on how to appreciate the varied exhibits were always most worthwhile and enriched my stays there enormously.

John is a caring and supportive father taking a real interest in his daughters and always there to offer support and advice. He also understands their need for independence and supports them in their chosen careers. He is lucky in this in having Karen to support him at home.

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In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part One: Biographical Contributions

Chapter Three: A Letter from the Family

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Dear John,

I have been thinking of the fullness and depth of your career, and in doing so, I find that many memories of your mentors, colleagues, and friends are woven into the fabric of it.

My first thought is of Raymond Hatcher, who served as your master's adviser at the University of Wisconsin–Milwaukee and started you on your way in bryology. On an expedition to Juan Fernandez Islands with him, you met Henry Imshaug who later served as your Ph.D. adviser at Michigan State University. Before the move to East Lansing, we spent the summer at the University of Michigan's biological station, fondly referred to as "The Bug Camp" working with Howard Crum. At MSU, Henry and Doris Imshaug frequently invited "The Students" (Dick Harris, Karl Ohlsson, Ismael Landron, and Ron

Taylor) for one of Henry's famous travel slide shows.

One warm August day some 35 years ago, you met Louis Williams, chairman of the botany department at the Field Museum, and with the generosity of Donald Richards, you became a member of the botany staff. Other names that come to my mind from those first years include Dr. Pat and Viji, Dorothy, Alfreda, Bill Grime. Roberta, and Bob Stolze.

Your research in Australia and New Zealand has had a personal impact on our family. When Beth was only two years old, we traveled with you and spent six months in Tasmania and other parts of Australia. Your sister, Mary Jean, joined us and became your collecting buddy. Des and Hilda Barker, Noel and Joel Kemp, Alan and Carolyn Canty, Rob and Gwen Seppelt, Buck and Joan Emberg, and of course our dear Maisie and Laurie Melbourne became lifelong friends.

The next trip we shared as a family was in 1984 when Laura was three and Beth seven. We spent three months in New Zealand. Our accommodations at Selwyn College in Dunedin were unique, to say the least. Do you remember the camping trip at Kelly's Creek in Arthur's Pass surviving that terrible storm in tents with lightning flashing and thunder echoing noisily against the mountains? John Child was your field companion and our family friend, and he showed us so many interesting sights. I know that Beth can still count from one to five in Maori, thanks to John. The warm friendships with Jan and Warren Dyer and the Lindsays have lasted over the years. The second part of the trip was spent in Tasmania, where old friendships were renewed. I can vividly remember Beth setting off to hike with you in her powder-blue field boots.

Laura joined you and Greg Mueller for a month in New Zealand the year she turned 18. In addition to enjoying the amazing scenery along

the many hikes you did together, she still treasures the memories of returning from Table Mountain well after dark, the beautiful tarns, spending time with the Braggins family, and learning the life skill of flipping and turning field-collecting packets. One never knows when that skill will be useful again. And of course, my latest memories are of the three weeks that we shared in the North Island of New Zealand in March 2007. You showed me what a paradise this beautiful country is. John and Thelma Braggins have been good friends. And last, but by no means least, the professional and personal relationship that you have with Matt von Konrat is most valuable.

And so, we thank you for giving us the gift of travel, exposing us to these amazing parts of the world, and letting us be a part of your professional life. May there be many more memories. We are very proud of you.

Love, Karen, Beth, and Laura

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Part Two: Bryophyte Life History

Chapter Four: Life Cycles in Major Lineages of Photosynthetic Eukaryotes, with a Special Reference to the Origin of Land Plants

Hilary A. McManus

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Chapter Four: Life Cycles in Major Lineages of Photosynthetic Eukaryotes, with a Special Reference to the Origin of Land Plants

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Abstract

Meiosis and fertilization represent two fundamental events in the origin, development, and evolution of the eukaryotic life cycle. A life cycle with alternation of generations evolved independently in multiple diverse eukaryote lineages, and variations of this type of life cycle can be found in the photosynthetic red, brown, and green algae and embryophyte land plants. The adaptive advantages of maintaining two multicellular stages necessary for sexual reproduction have been explored on both ecological and genetic levels. However, no hypothesis has been found to be applicable across the diverse lineages. This review summarizes the types of life cycles found in photosynthetic eukaryotes, focusing on those lineages that exhibit an alternation of generations and the adaptive advantages such life cycles may confer. The evolution of the embryophyte lineage and its transition from an aquatic to terrestrial habitat are discussed, as is how the first-diverging embryophyte lineage, the liverworts, display intermediate life cycle characteristics between those of their green algal ancestors and later-evolving embryophytes. In addition, the adaptive advantages of maintaining two multicellular stages are reviewed, particularly the evolution of a multicellular sporophyte through delayed zygotic meiosis and its resulting genetic complexity. The hypothesis developed by Svedelius in 1927 is favored that a lengthened diploid generation with simultaneous increase of the body size allows production of a large number of genetically different gametes via meiosis, which further leads to production of diverse offspring after fertilization.

Introduction

The evolution of a life cycle with alternating haploid and diploid generations in eukaryotes has received considerable attention throughout the past century (Svedelius, 1927; Stebbins, 1950; Searles, 1980; Bell & Koufopanou, 1991; Valero et al., 1992; Bell, 1994; Kondrashov, 1997; Mable & Otto, 1998; Graham & Wilcox, 2000b). Many hypotheses have been postulated and tested both theoretically and experimentally regarding the advantages and disadvantages of maintaining haploid and diploid stages (Lewis & Wolpert, 1979; Searles, 1980; Lewis, 1985; Kondrashov & Crow, 1991; Perrot et al., 1991; Valero et al., 1992; Orr & Otto, 1994; Perrot, 1994; Bell, 1997). Of particular interest has been the causes of multiple, independent trends toward evolution of alternation of generations within the photosynthetic eukaryotes (Rhodophyceae, Chlorophyta, Phaeophyceae) (Svedelius, 1927; Searles, 1980; Bell, 1994, 1997; Mable & Otto, 1998; Graham & Wilcox, 2000b) and the mechanisms by which this type of life cycle might have permitted successful colonization of land by the embryophytes (Bower, 1935; Campbell, 1940; Smith, 1955; Bell, 1994; Kenrick & Crane, 1997a; Graham & Wilcox, 2000b). This article first presents an overview of the various types of life cycles exhibited by major lineages of photosynthetic eukaryotes, particularly within the red, brown, and green algae. It then focuses on the evolution of alternation of generations along the charophyte-embryophyte lineage and discusses potential ecological and genetic advantages that this type of life cycle might have endowed on embryophytes that facilitated their successful colonization of land. Finally, it combines recent progress in phylogenetics and developmental biology and proposes several experimental schemes to test some ideas and hypotheses advanced earlier by others and those developed here.

Life Cycles of Major Photosynthetic Eukaryotes

Photosynthetic eukaryotes compose multiple evolutionary lineages distributed throughout the eukaryotic tree of life (Baldauf, 2003; Baldauf et al., 2004) (Fig. 1) that not only independently achieved their autotrophic abilities through primary, secondary, and tertiary endosymbiotic

events (McFadden, 2001; Grzebyk et al., 2003; Palmer, 2003; Yoon et al., 2004), but also developed a number of ways to complete their reproductive life cycles. Most sexual life cycles are typified by syngamy and meiosis linking growth and reproduction, and the length of time spent in each stage and the amount of growth that occurs vary widely across the lineages (Bell, 1994). Some life histories are considered haplobiontic, characterized by only one free-living stage. The free-living stage is either the gamete-producing, typically haploid stage, with the zygote representing the only diploid stage, or is the diploid stage, with the gametes representing the haploid stage. Many lineages of photosynthetic eukaryotes exhibit a haplobiontic life cycle dominated by the haploid stage, with the exceptions of the diatoms (Bacillariophyta), some brown algae (Phaeophyceae), and some green algae (Chlorophyta), which exhibit a diploid-dominant, haplobiontic life cycle (Fig. 1). Diplobiontic life histories, also known as alternation of generations, exhibit two multicellular stages with different ploidy levels (excluding the haptophyte group, Prymnesiophyceae, which alternate between haploid and diploid unicells, or motile stages that alternate with colonial or filamentous forms).

An alternation of generations was first recognized by Hofmeister in 1851 at the morphological level (see Hofmeister, 1862), and later Strasburger showed that the ploidy levels of the two stages are actually different (Strasburger, 1894). The generations are either of similar morphologies (isomorphic) and equal dominance or of different morphologies (heteromorphic) and one-stage dominant. In the case of alternation of heteromorphic generations, either generation may be free living or dependent on the other generation throughout its life span. Through mitosis, the gametophyte produces gametes that are released and subsequently fuse to form a diploid zygote. Mitotic divisions of the zygote result in the multicellular sporophyte stage, and through meiotic divisions spores are produced that give rise to the gametophyte stage (Fig. 2). Although the gametophyte generation is widely described as being haploid and the sporophyte as diploid, there is evidence of varying ploidy levels occurring in either stage of algae (Kuhlenkamp et al., 1993; Graham & Wilcox, 2000a), bryophytes (Smith, 1978; Crosby, 1979; Dyer & Duckett, 1984), ferns (Bower, 1923), and angiosperms (Grant, 1971; Bell & Koufopanou, 1991; Kondrashov, 1997).

However, for the purpose of this review, each generation is generally referred to as haploid (gametophyte stage) or diploid (sporophyte stage). Variations of this alternation of generations life cycle are exhibited in the red algae (Rhodophyceae), brown algae (Phaeophyceae), green algae (Chlorophyta and Charophyta), and the embryophyte land plants (Plantae), each of which is discussed here.

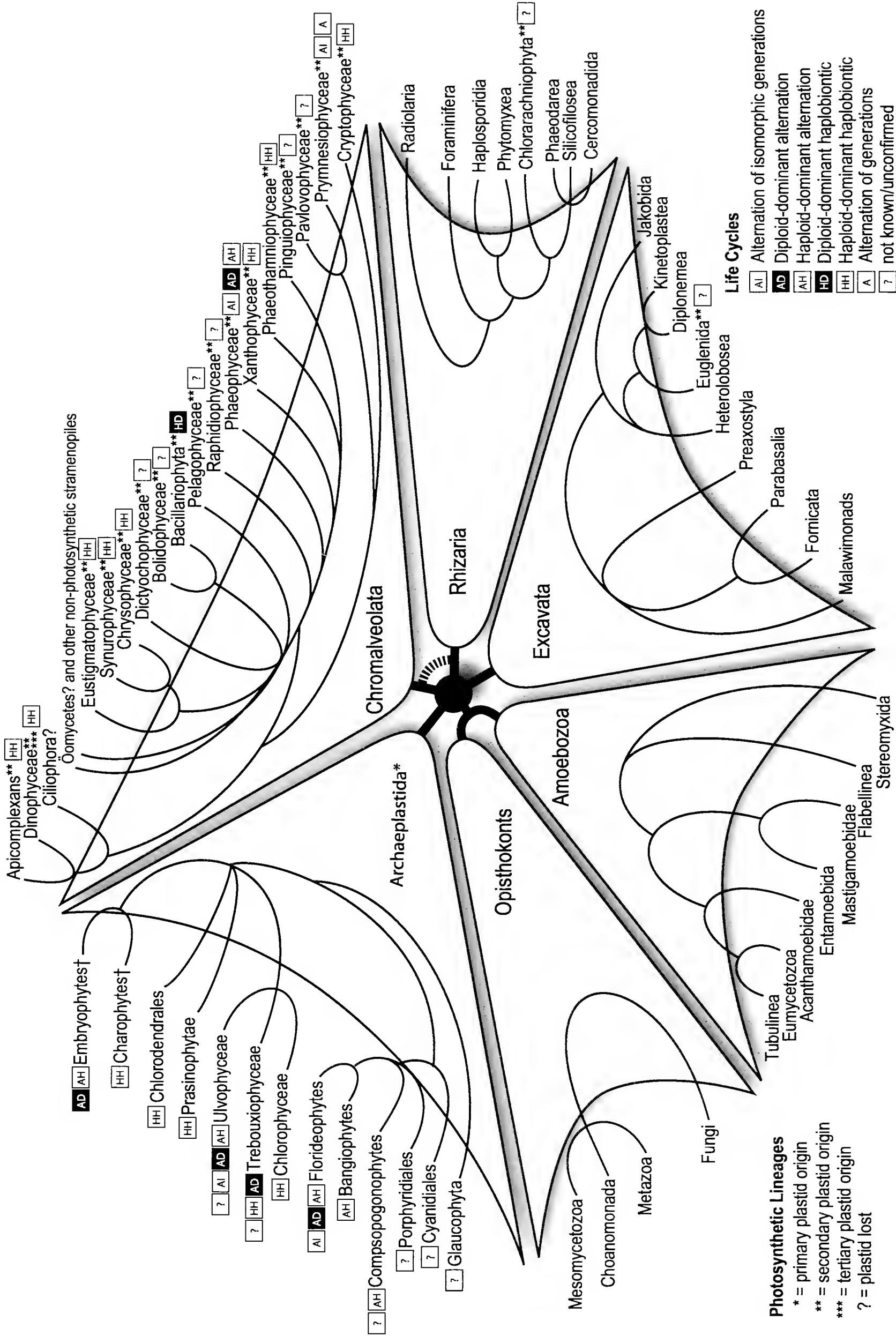
Rhodophyceae

The red algae form a lineage that is anciently related to the green algae and embryophyte land plants (Baldauf, 2003; Baldauf et al., 2004). The lineages for which sexual reproduction is known (bangiophytes, florideophytes, *Rhodochaete* Thuret ex Bornet) alternate either between a haploid and a diploid stage or between one haploid and two diploid stages, the latter also known as the triphasic life cycle (Fig. 1) (Bold & Wynne, 1985; Hommersand & Fredericq, 1990; Graham & Wilcox, 2000a). The triphasic life cycle is typical of the florideophyte red algae, where the first diploid phase, called the carposporophyte, is retained and develops on the haploid gametophyte (Bold & Wynne, 1985; Graham & Wilcox, 2000a). The retained carposporophyte is nourished via cell fusions by the gametophyte throughout its development, during which time it divides mitotically, amplifying the number of diploid carpospores that are produced. These diploid spores are released and develop into the second diploid phase, called the tetrasporophyte, which is free living. Some cells of the tetrasporophyte will undergo meiosis, producing haploid spores that give rise to the gametophyte stage. The majority of the florideophytes exhibit isomorphic gametophytes and tetrasporophytes, with only a few producing a larger gametophyte and even fewer with larger tetrasporophytes (some taxa in Nemaliales and Colaconematales). Some taxa even retain the tetrasporophyte on the gametophyte (e.g., *Devaleraea* Guiry and *Rhodochorton* Nägeli). The remainder of the red algae for which the sexual life cycles are known (bangiophytes) are heteromorphically biphasic and produce a gametophyte that is larger than the sporophyte (Bold & Wynne, 1985; Hommersand & Fredericq, 1990; Bell, 1994; Graham & Wilcox, 2000a; Guiry & Guiry, 2007). The phylogenetic relationships of the red algae are currently in a state of flux,

precluding formulation of any hypotheses regarding their branching order and evolution of life cycle types (Saunders & Hommersand, 2004; Yoon et al., 2004, 2006; Le Gall & Saunders, 2007). Although no evolutionary pattern toward the triphasic life cycle can be discerned, the development of a carposporophyte is regarded as a key innovation that allowed the florideophyte algae to diversify, resulting in thousands more species than bangiophyte red algae (Graham & Wilcox, 2000a).

Phaeophyceae

The brown algal lineage is nested within the stramenopiles of the eukaryote supergroup Chromalveolata (Baldauf, 2003; Andersen, 2004; Baldauf et al., 2004; Adl et al., 2005; Keeling et al., 2005; Hackett et al., 2007), and the taxa for which sexual reproduction is known exhibit both haplobiontic and diplobiontic life cycles (Fritsch, 1961; Wynne & Loiseaux, 1976; Bold & Wynne, 1985; Bell, 1994, 1997; Graham & Wilcox, 2000a; Cho et al., 2004; Adl et al., 2005; Guiry & Guiry, 2007). The diplobiontic brown algae exhibit life cycles of either free-living isomorphic generations (Sphacelariales, Tilopteridales, Dictyotales, most Ectocarpales, Ishigeales), diploid-dominant heteromorphic generations (Ascoseirales, Desmarestiales, Laminariales, Sporochnales, Syringodermatales), or in a few cases haploid-dominant heteromorphic generations (Scytosiphonaceae, Cutleriales). The gametophyte generation is reduced and dependent on the sporophyte in the Syringodermatales and Ascoseirales, with the most extreme case exhibited by the Fucales, in which the life cycle is typically considered diploid-dominant haplobiontic. The haploid generation (oogonia and antheridia) in the Fucales is retained on the diploid sporophyte (Wynne & Loiseaux, 1976; Clayton, 1984). Although the fuclean life cycle has been interpreted as diploid-dominant haplobiontic, some equate the oogonia with megasporangia that produce megagametophytes and the antheridia with microsporangia that produce microgametophytes, a characteristic of alternation of sporophyte and gametophyte generations in derived embryophyte land plants (Smith, 1955; Caplin, 1967; van den Hoek et al., 1995). The Fucales are thought to represent “the end of the line” in terms of gametophyte reduction in the brown algae (Clayton, 1984,



p. 27), and a recent molecular phylogeny of the Phaeophyceae supports the Fucales as one of the most derived lineages (Phillips et al., 2008). However, there is ambiguity regarding the exact relationships within the group (Kawai et al., 2007; Phillips et al., 2008), and any firm conclusion on the trend of evolution of life cycles will have to wait until a well-resolved phylogeny becomes available.

Chlorophyta

The lineages considered in this section are highlighted in Lewis and McCourt (2004) and Adl et al. (2005): Ulvophyceae, Chlorophyceae, Trebouxiophyceae, Chlorodendrales, and Prasinophytae. The Charophyta is excluded here but is discussed in the following section. The majority of the green algal lineages for which sexual reproduction is known (Chlorophyceae, Prasinophytae) exhibit haploid-dominant haplobiontic life cycles, with most of the haploid stages unicellular, colonial, or filamentous (Fig. 1). The Ulvophyceae consists of a mix of taxa with haplobiontic or diplobiontic life cycles, the latter showing alternation of isomorphic or heteromorphic generations, with parenchymatous and siphonous gametophytes and sporophytes (Bold & Wynne, 1985; Bell, 1994; van den Hoek et al., 1995; Graham & Wilcox, 2000a; Lewis & McCourt, 2004; Guiry & Guiry, 2007). Although the majority of ulvophytes for which sexual reproduction is known exhibit alternation of isomorphic generations, there are cases of heteromorphic, diploid-dominant life cycles (*Derbesia* Solier in Caulerpales). However, the life cycles and ploidy levels are relatively poorly known, and additional studies are needed for a more complete understanding of the dominant type of life history and possible evolutionary trends within the ulvophyte lineage (Kapaun, 1994; Graham & Wilcox, 2000a).

Sexual reproduction is not known for most of the trebouxiophytes, but some of the Prasiolales (*Prasiola* C. Agardh) are recorded to exhibit a diploid-dominant alternation of generations, producing parenchymatous sporophytes and filamentous gametophytes (Friedmann, 1959).

Charophyta

The charophyte algae are paraphyletic to embryophyte land plants (Pickett-Heaps, 1975; Graham et al., 1991; Karol et al., 2001; Qiu et al., 2006, 2007; Turmel et al., 2007) and consist of the remaining green algal lineages that were not included in the Chlorophyta: Mesostigmato-phyceae, Chlorokybophyceae, Klebsormido-phyceae, Zygnemophyceae, Coleochaetophyceae, and Charophyceae (Lewis & McCourt, 2004; Adl et al., 2005). As in the Chlorophyta, the charophyte algae exhibit haploid-dominant, haplobiontic life cycles. The growth forms include unicellular flagellates, sarcinoid packets, filaments, discs of cells, and branching thalli (Bold & Wynne, 1985; Bell, 1994; Graham & Wilcox, 2000a; Guiry & Guiry, 2007). Meiosis is zygotic, and the zygote is typically dispersed before releasing spores. In *Coleochaete* Brébisson, however, the zygote is retained on the gametophyte, and nourishment is thought to occur via gametophytic wall ingrowths surrounding the zygote (Graham & Wilcox, 1983, 2000b), but the zygote is still dispersed before spores are released. Three phylogenetic analyses of multigene data sets of the charophyte algae and embryophytes placed the Charophyceae as sister to the embryophytes (Karol et al., 2001; Qiu et al., 2006, 2007). Two recent studies using chloroplast genome sequences and genomic structural characters have challenged this placement and recovered the Zygnemophyceae (Charophyta) as the sister group to embryophytes (Turmel et al., 2006, 2007). However, this latter result might represent

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FIG. 1. The tree of eukaryotes depicting the six “supergroups,” highlighting the photosynthetic lineages and life cycle types of the photosynthetic lineages. Although not indicated, some lineages are paraphyletic with respect to one another. This tree is a summary constructed using phylogenies, classifications, and life cycle descriptions from the following references: Bell (1994), Kondrashov (1997), Graham and Wilcox (2000), Kawachi et al. (2002), Baldauf (2003), Andersen (2004), Baldauf et al. (2004), Houdan et al. (2004), Lewis and McCourt (2004), Saunders and Hommersand (2004), Adl et al. (2005), Andersson et al. (2005), Keeling et al. (2005), Simpson et al. (2006), Hackett et al. (2007), and Rodriguez-Ezpeleta et al. (2007a). † = According to Adl et al. (2005), the Embryophyte (also known as Plantae) lineage is grouped within the Charophyta (Chloroplastida) as a member of the subdivision Streptophytina. Depicted here is a lineage labeled Charophytes, representing all the algal lineages within the Charophyta as well as *Mesostigma* (Rodriguez-Ezpeleta et al., 2007b), and Embryophytes are illustrated separately for the purpose of this review.

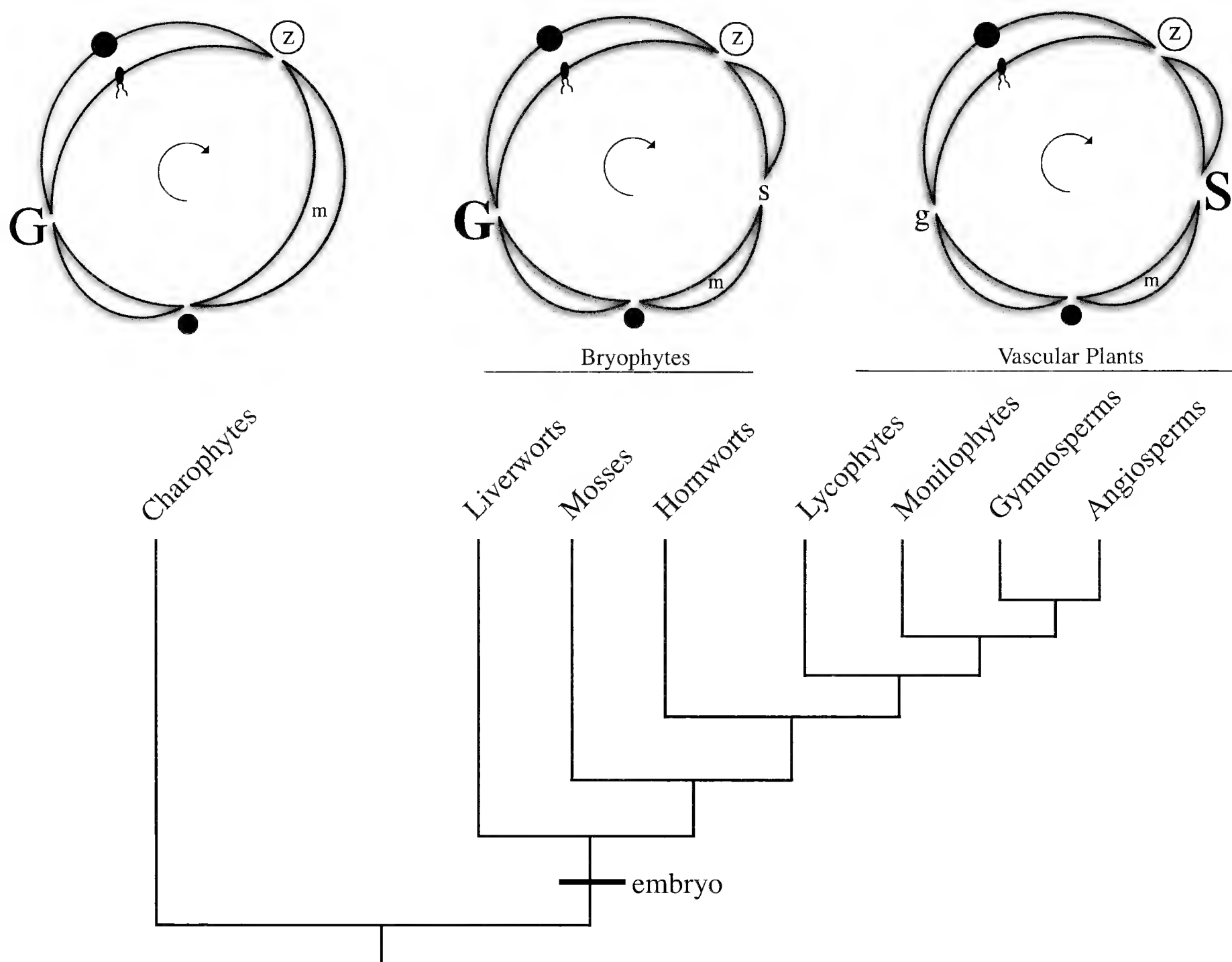


FIG. 2. Summary of the phylogenetic relationships of the charophyte algae and the embryophyte land plants based on Qiu et al. (2007) and their respective general life cycles. G = dominant gametophyte, z = zygote, m = meiosis, s = dependent sporophyte, g = reduced gametophyte, S = dominant sporophyte.

an analytical artifact due to taxon sampling insufficiency (Leebens-Mack et al., 2005; Lemieux et al., 2007). Given the broader taxon sampling and the use of sequence data from three cellular compartments in the three multigene analyses (Karol et al., 2001; Qiu et al., 2006, 2007), the phylogeny that places the Charophyceae as sister to the embryophytes is used for this review.

Plantae

The colonization of land by the embryophytes and their subsequent diversification were permitted by the gain of a suite of characters that allowed them to adapt to life in a terrestrial habitat. These characters include roots and conducting tissues to absorb and transport water and nutrients, a cuticle (cutin) for protection from desiccation, production of flavonoids and phenolics that act as UV filters and microbial deterrents,

and symbiosis between plants and mycorrhizal fungi that facilitate uptake of water and nutrients from the soil (Kubitzki, 1987; Graham, 1993; Taylor & Taylor, 1993; Brundrett, 2002; Kottke & Nebel, 2005; Duckett et al., 2006; Wang & Qiu, 2006). In addition, there was a major shift in life history, which is one of the defining characters of the lineage. The embryophyte land plants are fundamentally distinguished from the green algae by the gametophytic retention and matrotrophy of the developing embryo, which undergoes mitotic divisions to produce a multicellular sporophyte. To accurately trace this evolutionary transition along the charophyte-embryophyte lineage, it is integral to have an understanding of the phylogenetic relationships of the earliest-diverging embryophytes and their life histories.

Resolving the relationships among the lineages of the first-diverging embryophytes, the bryophytes (mosses, liverworts, hornworts), has been an issue of debate with different hypotheses

using various combinations of morphological, ultrastructural, physiological, biochemical, and molecular characters (Mishler & Churchill, 1984; Garbary et al., 1993; Lewis et al., 1997; Renzaglia et al., 2000). Several studies recovered the liverworts as the earliest-diverging embryophyte lineage (Mishler & Churchill, 1984; Bremer, 1985; Mishler et al., 1994; Kenrick & Crane, 1997b; Lewis et al., 1997; Qiu et al., 1998), and liverwort-like spores recently described from Ordovician sediments support the liverworts as the first-divergent embryophyte land plants (Wellman et al., 2003). Further, several studies analyzing extensive molecular data sets have placed hornworts as sister to vascular plants (Lewis et al., 1997; Samigullin et al., 2002; Dombrovskaya & Qiu, 2004; Kelch et al., 2004; Groth-Malonek et al., 2005; Wolf et al., 2005; Qiu et al., 2006, 2007). Although it cannot be said that relationships among the early-diverging lineages of land plants are conclusively resolved, they are probably robust enough to serve as a hypothetical framework to allow comparative analysis of life cycle evolution in early embryophyte land plants.

The three lineages of bryophytes all exhibit gametophyte-dominant alternation of generations and a multicellular sporophyte that is retained and nourished on the gametophyte but of varying degrees of size and levels of dependency. The liverwort sporophyte is typically enclosed in gametophytic tissue, which supplies water and nutrients and keeps it sheltered from environmental stresses during its development; the sporophyte emerges just prior to spore dispersal (Schuster, 1992; Crandall-Stotler & Stotler, 2000; Renzaglia et al., 2000, 2007; Crum, 2001). The moss sporophyte grows as an erect stalk from the archegonium on the gametophyte and is capable of photosynthesis, though it remains dependent on the gametophyte for its nutrition until shortly before sporogenesis (Bold, 1940; Paolillo & Bazzaz, 1968; Renzaglia et al., 2000; Crum, 2001; Stark, 2002). The hornworts produce a persistently chlorophyllous, erect sporophyte that is retained and also receives nourishment from the gametophyte. It has been shown that the hornwort sporophyte can outlive the gametophyte and is therefore capable, to some degree, of obtaining nutrients independently (Campbell, 1924; Stewart & Rodgers, 1977; Schuster, 1992; Renzaglia et al., 2000; Crum, 2001).

The transition of the diploid stage represented by a unicellular zygote in the charophytes to a multicellular sporophyte in the bryophytes required a number of steps, beginning with

retention of the zygote on the gametophyte, matrotrophy, then delayed zygotic meiosis, and ultimately resulting in a multicellular sporophyte (Fig. 2). The sister group to the embryophytes exhibits retention of the zygote, and in *Coleochaete* there is evidence of the gametophyte supplying nutrients to the zygote before its release and subsequent germination (Graham & Wilcox, 2000b; Karol et al., 2001). The life history characteristics of the liverworts would represent the next step along the progression of sporophyte multicellularity, with its small, dependent sporophyte, and further transitions toward more complex and less dependent sporophytes found in the mosses and hornworts.

Origin of the Embryophyte Life Cycle

The debate about the origin of alternation of generations in the embryophytes has centered around two theories postulated over the years, each receiving its own support based on the fossil record or the resolution of phylogenetic relationships (Celakovsky, 1874; Pringsheim, 1878; Bower, 1890, 1908, 1935; Zimmermann, 1930; Campbell, 1940; Smith, 1955; Graham, 1993; Remy et al., 1993; Taylor & Taylor, 1993; Kenrick & Crane, 1997a; Graham & Wilcox, 2000b; Karol et al., 2001; Taylor et al., 2005; Gerrienne et al., 2006; Qiu et al., 2006, 2007). Both theories consider the ancestral condition of the embryophyte life cycle to occur within the algae, either in lineages containing alternation of isomorphic generations (Ulvophyceae: *Ulva* L.) or the gametophyte-dominant haplobiontic life cycle (Charophyceae).

The antithetic theory (Celakovsky, 1874; Bower, 1908, 1935; Campbell, 1940; Smith, 1955) suggests a green algal ancestor that exhibits a gametophyte-dominant haplobiontic life cycle and a unicellular zygote that undergoes meiosis, such as that found in extant charophyte algae. The transition onto land by this lineage was accompanied by the retention and nourishment of the zygote and delayed meiosis, resulting in development of a multicellular sporophyte through mitotic divisions. Along the embryophyte lineage, continued mitotic divisions in the sporophyte lead to an increase in body size and eventual increased complexity such as found in the tracheophytes. Recent phylogenetic analyses support a relationship between the charophyte

algae and embryophytes as well as the paraphyly of bryophytes to tracheophytes, thus revealing the intermediate steps in the transition from a unicellular zygote in green algae through a more complex but generally gametophyte-dependent sporophyte in bryophytes to an independent, free-living sporophyte in tracheophytes (Mishler & Churchill, 1984; Graham et al., 1991; Kenrick & Crane, 1997a; Karol et al., 2001; McCourt et al., 2004; Qiu et al., 2006, 2007).

The homologous theory (Pringsheim, 1878; Zimmermann, 1930) proposed that the ancestors to embryophytes were algae with alternation of isomorphic generations and that there was a transition from two free-living stages to the gradual reduction and subsequent dependence of the gametophyte stage and increased complexity of the sporophyte stage. The proponents of this hypothesis did not consider the bryophyte lineages as intermediate steps to the vascular plants but rather as a distinct line of evolution after algae colonized the land. The line leading to the bryophytes involved the reduction and eventual dependence of the sporophyte on the gametophyte, whereas the other resulted in the reduction and final dependence of the gametophyte on the unreduced, free-living sporophyte, represented in the tracheophytes. The exquisite fossils of gametophytes and sporophytes unearthed from the Devonian Rhynie Chert were interpreted as evidence to support the homologous theory (Graham, 1993; Remy et al., 1993; Taylor & Taylor, 1993; Kenrick & Crane, 1997b; Kenrick, 2000; Taylor et al., 2005). However, the earliest land plant fossil records indicate that land plants originated in the Middle Ordovician (Gray, 1993; Wellman et al., 2003). Hence, the Rhynie Chert fossils probably represent lineages that arose well after the transition to land; thus, their characteristics may have little significance in supporting the homologous theory regarding the origin of alternation of generations in embryophyte land plants. Further, a recent study has shown that Devonian plants might have exhibited a heteromorphic alternation of generations in addition to an isomorphic one as shown by those from the Rhynie Chert (Gerrienne et al., 2006). Finally, the massive amount of morphological, ultrastructural, biochemical, and molecular evidence gathered over the past three decades (Pickett-Heaps, 1975; Mishler & Churchill, 1984; Graham et al., 1991; Kenrick & Crane, 1997a; Lewis et al., 1997; Karol et al., 2001; Samigullin et al., 2002; Dombrowska & Qiu, 2004; Kelch et al., 2004; McCourt et al.,

2004; Groth-Malonek & Knoop, 2005; Wolf et al., 2005; Qiu et al., 2006, 2007) favors the antithetic theory over the homologous theory. The homologous theory does, however, seem to leave one possibly valid intellectual heritage, that is, genetic similarity and homology (not orthology) between the gametophyte and the sporophyte (see Crum, 2001), as is shown by a recent study that demonstrates the homologous genetic basis underlying rhizoid and root hair development in *Physcomitrella patens* (Hedw.) Bruch & Schimp. and *Arabidopsis thaliana* (L.) Heynh., respectively (Menand et al., 2007).

Adaptive Advantages of Alternation of Generations

The maintenance of life cycles that alternate between two multicellular stages with different ploidy levels in multiple lineages of photosynthetic eukaryotes indicates that it confers adaptive advantages. Various hypotheses have been formed and tested, particularly on the development and maintenance of a diploid multicellular sporophyte stage, at both genetic and ecological levels. Valero et al. (1992), Perrot (1994), Mable and Otto (1998), and Zeyl (2004) provide summaries of these hypotheses as well as theoretical and empirical evidence that have been obtained for or against them. This section includes a brief review of some of these hypotheses and highlights the most favored hypothesis in light of our new understanding of the branching order of the first-diverging embryophytic land plants.

Ecological Hypotheses

VARYING ECOLOGICAL NICHES—One of the most discussed ecological hypotheses regarding maintaining a life cycle with alternation of generations considers the ability of each stage to fill a different ecological niche and therefore to survive various selection pressures (Stebbins & Hill, 1980; Keddy, 1981; Klinger, 1993; John, 1994; Perrot, 1994). Several studies indicate that this may be the case in the brown and red algae, even for those with isomorphic generations (Clayton, 1988; Destombe et al., 1993; Hughes & Otto, 1999). Herbivore grazing, seasonal changes, and environmental fluctuations are likely influencing

the heteromorphic generations in brown algae (Lubchenco et al., 1980; Slocum, 1980; Littler & Littler, 1983; Clayton & Lloyd, 1985); the isomorphic or slightly heteromorphic stages in red algae (Edwards, 1973; Destombe et al., 1993; Ross et al., 2003; Thornber & Gaines, 2004) and unicellular, heteromorphic stages of some prymnesiophytes (Houdan et al., 2006) fill different ecological niches. The extreme reduction of the haploid stage in the Fucales is thought to be in response to the harsh intertidal habitat, retaining and protecting the haploid generation on the diploid phase during the alternating periods of desiccation and wetting, and the increased exposure to UV radiation before dispersal for fertilization (Delf, 1939; Clayton, 1984). With the move onto land in the early lineages of embryophytes, the bryophyte sporophyte is dependent on the gametophyte, and therefore both appear to inhabit the same ecological niche and experience similar selection pressures. However, the sporophyte increases in size along the embryophyte lineage, rising above the ground to facilitate spore dispersal, while the gametophyte remains where it is likely to be exposed to water necessary for the flagellated gametes to swim during sexual reproduction (mosses, hornworts, ferns) or gradually becomes reduced and dependent on the sporophyte (gymnosperms, angiosperms) (Keddy, 1981).

The nutrient-limiting hypothesis (Lewis, 1985) proposes that the haploid stage grows better under nutrient-poor conditions, needing fewer nutrients since it contains only half the DNA found in diploids. Experimental tests recover mixed results, supporting the nutrient-limiting hypothesis using isomorphic stages of *Gracilaria* Greville (Rhodophyceae) (Destombe et al., 1993) and producing varying results in experiments utilizing the yeast *Saccharomyces cerevisiae* Meyen ex E.C. Hansen (Roman et al., 1955; Fowell, 1969; Adams & Hansche, 1974; Weiss et al., 1975; Glazunov et al., 1989; Naidkhardt & Glazunov, 1991; Mable, 2001; Zeyl, 2004). Evidence suggests that nutrient availability may play a role in driving the evolution and maintenance of two or more multicellular stages, but further studies are needed in additional groups of organisms for a better understanding of this hypothesis.

MATROTROPHY AND DELAYED MEIOSIS—Graham (1993) suggested that the increased availability and rapid diffusion of CO₂ and a higher level of solar radiation on land, compared with the aquatic environment inhabited by the

charophyte ancestors of embryophytes, was a driving force in the jump to a terrestrial habitat along the charophyte-embryophyte lineage. In response, strategies to survive the new environmental stresses were necessary for the embryophytes to succeed (Graham, 1993; Crum, 2001). Although other lineages of green algae also made a transition onto land without a drastic change in their life cycle (e.g., desert green algae), the shift from a haploid-dominant haplobiontic life cycle found in the putative charophyte ancestor to a haploid-dominant diplobiontic life cycle in bryophytes is correlated with the embryophyte move to the harsh terrestrial environment. The haplobiontic life cycle results in relatively few spores, generally four, from each zygote that undergoes meiosis. However, some charophyte taxa are known to produce larger zygotes that can give rise to anywhere from 8 to 32 spores (Graham & Wilcox, 1983, 2000a). The larger zygotes therefore may require more nutrition; thus, retaining and nourishing each zygote ensures its survival and improves the chances of successful spore dispersal (Graham & Wilcox, 1983; Graham, 1993).

The matrotrophic nature of the embryo and subsequent development of a multicellular sporophyte via delayed meiosis as observed in the bryophytes amplifies the products of fertilization through the mitotic growth of the sporophyte, resulting in a larger number of cells that can undergo meiosis to produce spores. It has been suggested that this retention of the embryo and development of many spores is in response to sexual reproduction in the bryophytes being limited by water availability (Svedelius, 1927; Bower, 1935; Searles, 1980). Since water availability in a terrestrial habitat may limit the number of fertilization events (via flagellated sperm swimming to the egg), retention and nourishment of the embryo would increase the survival rate of the offspring. The large number of spores produced by the sporophyte would compensate for the low or variable rates of fertilization events and dispersal of spores into uninhabitable environments (Svedelius, 1927; Bower, 1935; Searles, 1980; Crum, 2001). Searles (1980) equated this adaptation to the triphasic life cycle in the red algae, a group characterized by nonflagellated sperm that are therefore randomly carried to the nonmotile egg via water currents during sexual reproduction. Development of a gametophyte-dependent carposporophyte that increases the number of carpospores produced through mitotic divisions, followed by production of tetrasporophytes from

the carpospores that subsequently gives rise to multiple haploid spores, compensates for low fertilization rates (Searles, 1980). This hypothesis has since received support in a theoretical study on phase dominance in red algae (Fierst et al., 2005).

Genetic Hypotheses

The genetic arguments for maintaining alternation of generations have traditionally centered around the adaptive advantages of diploidy, and it is thought that there is an evolutionary trend from haploid dominance to diploid dominance. However, the phylogenetic pattern of ploidy dominance in groups of organisms that exhibit the various forms of alternation of generations (Phaeophyceae, Rhodophyceae, Chlorophyta) (Fig. 1) is currently not clear because of a lack of well-resolved phylogenies, with the exception of the charophyte/embryophyte lineage. Therefore, a focus on the adaptive advantages of diploid dominance along the embryophyte lineage is the main focus of this section.

Some of the hypotheses favoring the diploid condition based on arguments from genetics include the ability of diploids to mask the effects of deleterious mutations (Crow & Kimura, 1965), the accumulation of beneficial mutations at a higher rate than their haploid counterpart (Paquin & Adams, 1983), the ability of diploids to more easily enlarge their genomes with new genes for new functions (Lewis & Wolpert, 1979), and the ability for diploids to achieve increased complexity (tissue differentiation) (Raper & Flexer, 1970; Maynard-Smith, 1978). A comparatively more UV-rich and mutagenic terrestrial environment may be consistent with the evolution of an extended diploid phase in the life cycle of embryophyte land plants. However, the proposed advantages of masking deleterious mutations have since been theoretically tested, and the results indicate the advantages are transitory in the individual. Thus, masking does not always favor diploidy and can be disadvantageous for the offspring where the deleterious mutations accumulate (Kondrashov & Crow, 1991; Perrot et al., 1991; Otto & Goldstein, 1992). The presence of two copies of each gene was thought to contribute to a faster rate of accumulation of beneficial mutations and therefore faster rates of adaptation to environmental changes (Paquin & Adams, 1983).

Although a case can be made that diploids are likely to carry new beneficial mutations, masking of these mutations may actually result in slower rates of accumulation in the diploids, favoring the haploid (Orr & Otto, 1994; Mable & Otto, 1998).

The presence of two alleles in a diploid may allow, through the modification of one allele, its maintenance via heterosis and subsequent gene duplication, the evolution of new gene functions without significant negative impact on the organism (Lewis & Wolpert, 1979). A haploid will be able to evolve new genes with new functions (while maintaining old gene functions) only through first gene duplication, followed by mutation (Lewis & Wolpert, 1979).

There is also a pattern of gene recruitment from the gametophyte, or haploid, generation to the sporophyte generation in embryophyte land plants. Some examples include MADS-box genes located in the haploid stage of charophycean algae but in the sporophyte (diploid) stage of vascular plants (Tanabe et al., 2005) and the presence of transcription factors involved in root hair development found in the *Arabidopsis* sporophyte stage yet in the gametophyte stage of *Physcomitrella* (Menand et al., 2007). Such discoveries indicate that evolution of a multicellular, complex sporophyte in the embryophytes was likely aided by the recruitment of regulatory genes from the gametophyte to the sporophyte (Tanabe et al., 2005; Menand et al., 2007; Nishiyama, 2007). Examples of co-option and subfunctionalization abound, lending support to a genetically based homologous theory.

The hypothesis of increased capacity for genome expansion and new gene functions of the diploid (Lewis & Wolpert, 1979) could complement the hypothesis that diploidy allows the achievement of increased complexity and tissue differentiation put forward by Maynard-Smith (1978) and Raper and Flexer (1970). Although there certainly are exceptions (unicellular diatoms, red algal tetrasporophytes) to the hypothesis that diploid stages exhibit tissue differentiation and overall increased complexity, this does appear to be the trend in the Phaeophyceae as well as along the embryophyte land plant lineage. The diploid-dominant brown algae typically have larger and more complex thalli in which cell differentiation has occurred, such as meristems and conducting cells (e.g., Laminariales, Desmarestiales), and even more complex forms in the lineages with a reduced, dependent haploid stage (Syringodermatales, Ascoseirales, Fucales).

The structurally complex fucalean lineage is the most successful in the intertidal zone, able to survive the harsher conditions of periodic freezing, desiccation, and exposure to UV radiation. The evolution of this particular brown algal life history and its global success in the harsh environment of the intertidal zone has been hypothesized to be analogous to the evolution of the dominant and structurally complex sporophytes in derived embryophyte land plants (Clayton, 1988). The conferred increased capacity of diploidy to develop new gene functions permitted the production of more complex forms and cell differentiation, leading to the development of traits that allowed the sporophyte to adapt to harsher, drier habitats. This is apparent along the embryophyte lineage, with the sporophyte becoming larger, more complex, and better adapted to drier habitats than the haploid gametophyte stage.

Summary

The multiple, independent origins of a life cycle that alternates between two multicellular stages with different ploidy levels in eukaryotes suggests that this type of life cycle must confer certain adaptive advantages and thus calls for an explanation. Both ecological and genetic aspects have been considered in various hypotheses that attempt to explain this evolutionary phenomenon, but none seems to be applicable across the diverse lineages. Therefore, we find it necessary to revive a hypothesis formulated by Svedelius in 1927 that proposed that a fundamental advantage of diploidy over haploidy is that meiosis occurs in the diploid stage of the life cycle. Under any environmental selection, an extended diploid phase coupled with size increase of the organism magnifies the number of cells that can undergo meiosis to form genetically different gametes via crossing over between chromatids and independent assortment of homologues of different chromosome pairs. The random reunion of genetically different gametes during fertilization further leads to the production of genetically variable offspring. The resulting genetic variability then confers adaptive advantages to the offspring, permitting them to readily adapt to various selective pressures, both ecological and genetic, as discussed previously.

Indeed, the advantage of a large number of genetically variable gametes produced by a

multicellular diploid stage has been manifested in red algae, where lack of flagella most likely limited the number of fertilization events (Searles, 1980), and in land plants, where lack of water limits the ability of flagellated sperm to migrate to the egg (Svedelius, 1927; Bower, 1935; Stebbins, 1950). The advantage of producing genetically variable gametes via meiotic events in a multicellular sporophyte leading to genetically diverse offspring cannot be realized in the haploid phase.

Although our focus has been on the advantages of the diploid stage, the retention and maintenance of the haploid stage in multiple algal lineages, as well as the free-living gametophyte generation in the bryophyte and monilophyte lineages, indicates that it also confers some adaptive advantages. The ulvophyte green algae mainly exhibit two free-living stages, and maintenance of the multicellular gametophyte stage has been hypothesized to be due to its advantage over unicellular gametophytes in producing a large number of gametes and therefore zygotes (Graham & Wilcox, 2000a), though the genetic diversity of gametes as well as offspring produced by this type of life cycle is much smaller than that produced by the life cycle seen in embryophytes. In the case of the bryophytes, not only could the maintenance of the multicellular gametophyte allow the capability of the production of a large number of gametes that then give rise to sporophytes, but the multicellular gametophyte supplies nutrition to the developing embryo and sporophyte, ensuring their survival and fitness; this is also the case for the red algae. Matrotrophy is apparent throughout the embryophytes, even in the gymnosperms and angiosperms in which the gametophyte tissue (megagametophyte and endosperm, respectively) supplies nutrition to the developing embryo. Since the sporophyte of the bryophytes has not yet developed the capacity to independently occupy a drier habitat, maintaining the gametophyte stage is integral for its survival.

Future Directions

Alternation of generations represents a transitional state in life cycle evolution in eukaryotes where two key events, meiosis and fertilization, and the evolutionary genetic advantage of the diploid phase preset the stage for life cycle evolution from a haploid- to a diploid-dominant state, resulting in multicellularity and genetic

complexity. The recent resolution of the phylogenetic relationships of the most basal lineages of the embryophyte land plants, the bryophytes (Qiu et al., 2007), as well as those of the charophyte algae (Karol et al., 2001), forms a solid framework to study the evolutionary history of molecular and developmental characters that were involved in the transition from a haplobiontic life cycle in the charophytes to the diplobiontic life cycle of the embryophyte land plants. The traits necessary for this transition—zygote retention, matrotrophy, and particularly delayed (zygotic) meiosis and root morphogenesis in the sporophyte—are important targets in the quest to better understand the genetic basis and evolution of the embryophyte life cycle.

A delay in meiosis, which resulted in the development of a multicellular diploid stage, indicates that the genes controlling the timing of meiosis were directly under selection during the development of multicellular diploid stages in multiple lineages of eukaryotes. The mechanisms for the cell cycle switch from mitosis to meiosis have been extensively studied in the fission yeast *Schizosaccharomyces pombe*. Multiple genes were described that are involved in controlling the different stages of meiosis, and in particular the *mei2* gene was found to encode a protein that is essential for premeiotic DNA synthesis and the commitment to meiosis (Bresch et al., 1968; Egel, 1973; Egel & Egel-Mitani, 1974; Iino & Yamamoto, 1985; Watanabe & Yamamoto, 1994). A survey of available sequences in databases by Jeffares et al. (2004) revealed that *mei2*-like genes occur in fungi, chromalveolates, an early-branching entamoebidae *Entamoeba histolytica* Schaudinn, and embryophytes. The phylogenetic distribution of the gene indicates that it originated early in eukaryote evolutionary history and was subsequently lost in some lineages, including the metazoans, while it diversified in plants (Jeffares et al., 2004).

The number of *mei2*-like gene copies increases along the embryophyte lineage, and two main groups have been recovered. Whereas one group of *mei2*-like genes has been shown to be involved in cell differentiation, expressed in shoot and root meristems rather than in cells undergoing meiosis (Veit et al., 1998; Jeffares et al., 2004), the other group plays a role in the vegetative meristem as well as meiocytes in *Arabidopsis thaliana* (Kaur et al., 2006). These results suggest functional conservation in the genes controlling meiosis between yeast and plants.

An evolutionary development approach tracing the evolution and subfunctionalization

of *mei2*-like genes along the charophyte-embryophyte lineage will assist us in the process of pinpointing the evolutionary steps involved in the origination of the multicellular diploid stage. The liverwort life cycle represents an intermediate step between the ancestral charophyte algae and the later-branching embryophytes. Targeting the liverworts when studying the evolution of genes involved in the timing of meiosis will reveal critical historical points of meiotic gene duplication and subfunctionalization along the embryophyte lineage, which, when combined with habitat information, may in turn offer insight into the adaptive advantages of a multicellular diploid stage in embryophytes.

In addition to experimental approaches, compiling information regarding phylogenetic relationships of photosynthetic eukaryotes and their life cycle characteristics and overall natural history traits will be useful in further tests of the adaptive advantages of the various life cycle types. More resolved phylogenies are expected to become available in the near future, particularly as results of the National Science Foundation's "Assembling the Tree of Life" research funding program. Mapping life cycle types and natural history characteristics on well-resolved phylogenies can reveal evolutionary trends of life cycle types and habitat correlations in individual photosynthetic lineages. These types of data can also form the basis to test whether, as Svedelius hypothesized in 1927, there is an evolutionary trend from haplobiontic to diploid stage-dominant alternation of generations in the photosynthetic eukaryotes.

A third area of study will be to investigate lineages in which the maintenance of the multicellular haploid generation is rarely seen, such as in animals. Svedelius (1927) hypothesized that with the development of a larger, complex diploid generation that could give rise to genetically variable sexual gametes, the haploid generation became unnecessary and therefore was gradually reduced. The gradual reduction of the gametophyte stage can be traced along the embryophyte lineage, particularly in the more derived lineages, such as gymnosperms and angiosperms. The Fucales also exhibit a reduced gametophyte stage, though further investigations of their phylogenetic position are needed. Is the complete omission of the multicellular haploid generation the evolutionary pinnacle in the evolution of eukaryotic reproductive strategies? Can we trace transitional states of haploid stage reduction along the animal

lineage, as we see in the embryophytes? Further, as evolutionary changes continue to accumulate, can it be expected that the fate of the embryophyte gametophyte is complete omission? Fungi, particularly ascomycetes and basidiomycetes, exhibit an interesting life cycle variation with a relatively short or almost absent diploid stage. After sexual reproduction, they exhibit dikaryotic (karyotypically haploid but functionally diploid) hyphae until karyogamy, which is almost immediately followed by meiosis. Investigation of life cycles of diverse eukaryotes, guided by well-resolved phylogenies and niche information, will shed light on some of these questions, ultimately bringing a complete understanding on the evolution of life cycles in eukaryotes.

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Chapter Five: Distribution of Terpenoids and Aromatic Compounds in Selected Southern Hemispheric Liverworts

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Chapter Five: Distribution of Terpenoids and Aromatic Compounds in Selected Southern Hemispheric Liverworts

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Abstract

Bryophytes contain a large number of terpenoids and aromatic compounds. In this article, the chemical constituents of selected liverworts collected in New Zealand, Malaysia, Madagascar, Argentina, Ecuador, and other southern hemispheric countries are discussed. The southern hemisphere is a region of extraordinarily high liverwort diversity. Many of compounds isolated from these liverworts have been represented by novel carbon skeletons and are important chemical markers of a liverwort's genus or family. Many of these compounds also have interesting biological activity.

Introduction

Liverworts, among green plants, are generally regarded as the simplest of extant terrestrial

plants. Although liverworts are morphologically very small and almost useless in a human diet, there are a number of terpenoids and aromatic compounds, including several new carbon

skeletons. It is quite noteworthy that some species belonging to the same genus produce normal or enantiomeric terpenoids. Some liverworts elaborate both enantiomers of the same compounds. The knowledge of their chemical constituents might serve to delineate not only chemical but also evolutionary relationships within the Marchantiophyta at the genus or family level. Several compounds present in liverworts show interesting biological activity, such as antimicrobial, antifungal, antiseptic, antihepatotoxic, cytotoxic, antioxidant, cardiogenic, insect antifeedant, and muscle-relaxing activity (Asakawa, 1982a, 1995, 2007). Terpenoids and lipophilic aromatic compounds are produced in the secretory apparatus of liverworts. The other two divisions of bryophytes (Bryophyta and Anthocerotophyta) contain no oil bodies. Oil body morphology of the Marchantiophyta together with their chemical constituents are significant indicators for the taxonomy of liverworts (Asakawa, 1982b; Asakawa et al., 1996).

Liverworts are distributed worldwide, though most commonly found in the tropics. The southern hemisphere is a region of extraordinarily high liverwort diversity. This hemisphere has more (numerous) endemic liverwort species than the northern hemisphere, including Japan (Inoue, 1988). There is a theory that the origin of bryophytes is to be found in the southern hemisphere (Inoue, 1988; Asakawa et al., 1996). From the viewpoint of the evolution and differentiation of (the) bryophyte(s) species, analysis of the liverworts growing in the southern hemisphere is important. A study of the southern hemispheric species may tell us more about the phylogeny and origins of liverworts as a whole. In this present review, we wish to summarize the distribution of terpenoids and aromatic compounds in selected southern hemispheric liverworts together with their chemosystematics and biological activity.

Materials and Methods

Each liverwort was dried and mechanically ground, followed by extraction with diethyl ether or methanol for 7–30 days. Each extract was filtered and the solvent evaporated to give green oils that were analyzed directly by thin-layer chromatography (TLC) and gas chromatography/mass spectrometry (GC/MS). TLC was carried out on precoated plates (silica gel: Merck GF254,

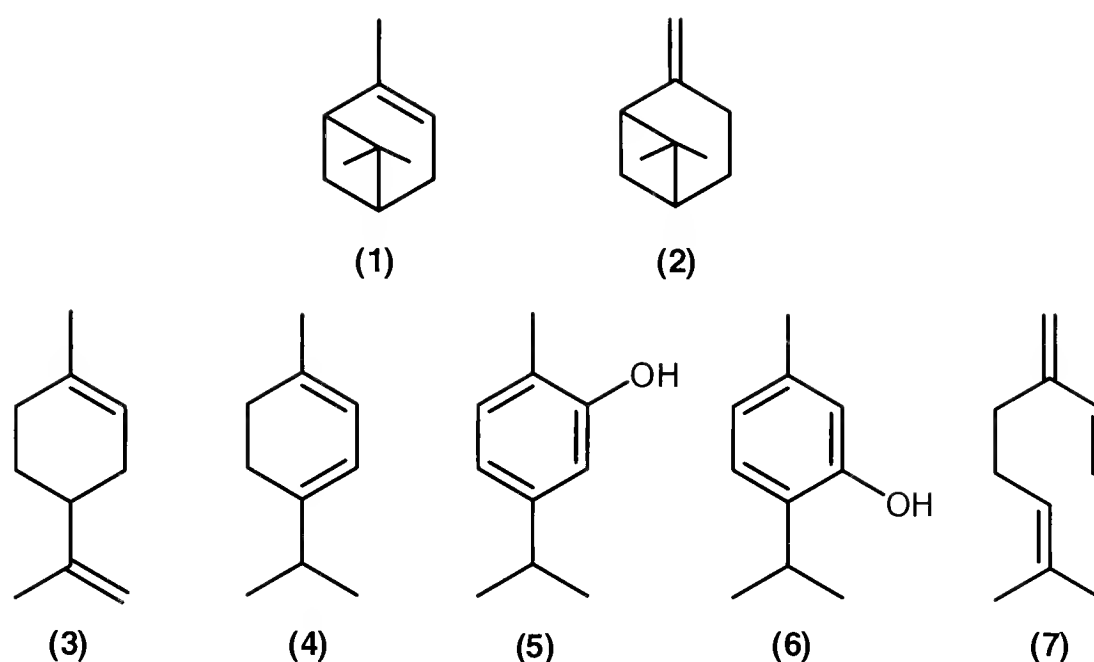
0.25 mm; CN: Merck F254 s, 0.2 mm; or RP-18: Merck F254 s, 0.25 mm) in different solvent systems. The spots on TLC were confirmed by spraying with Godin reagent and heated to 100–110°C. The GC/MS of the ether extracts were carried out using Hewlett-Packard HP-5971A or HP-5972A gas chromatographs coupled with mass selective detector and on DB-17 capillary column (0.25 mm × 30 m, 0.25-mm thickness) using helium as the carrier gas (1 ml/min). Oven temperature was 50–250°C temperature programmed at 5°C/min. Injection temperature was 250°C. The remaining extracts were chromatographed on silica gel or Sephadex LH-20 using *n*-hexane-ethyl acetate gradient and methanol-chloroform (1:1) as eluents, respectively. Each fraction was purified by a combination of preparative TLC and preparative high-performance liquid chromatography or middle pressure column chromatography. The structures of the isolated compounds were determined by ¹H- and ¹³C-NMR spectroscopies and X-ray crystallographic analysis.

MATERIAL EXAMINED—Ninety liverwort species, including 39 genera, were collected in Argentina, Australia, Bolivia, Colombia, Ecuador, Madagascar, Malaysia, New Zealand, Panama, Peru, South Africa, Taiwan, and Venezuela. All liverwort samples were identified and their voucher specimens have been deposited in the Faculty of Pharmaceutical Science, Tokushima Bunri University, Japan.

Chemical Constituents of Southern Hemispheric Liverworts

Monoterpenoids

Some liverwort species emit an intense fragrant odor on being crushed. Such a fragrance is generally due to monoterpenoids. The monoterpenoids found most frequently in liverworts are α -pinene (1), β -pinene (2), and limonene (3) (Asakawa, 1995). Among the southern hemispheric liverworts investigated, α -pinene (1) was detected in *Frullania falciloba* Taylor ex Lehm. from Australia (Asakawa et al., 1987a) and New Zealand (Asakawa et al., 2003), in *Dendromastigophora flagellifera* (Hook.) R.M. Schust. from New Zealand (Asakawa et al., 1996), and in *Omphalanthus filiformis* (Sw.) Nees (Asakawa & Inoue,



1987a), *Plagiochila pachyloma* Taylor, *P. oresitropa* Spruce, and *P. verruculosa* R.M. Schust. from southern Peru (Asakawa & Inoue, 1987b). In two New Zealand *Frullania* species—*F. pycnantha* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees and *F. spinifera* Taylor and also in *Plagiochila stephensoniana* Mitt.— α - (1) and β -pinene (2) were detected (Asakawa & Campbell, 1982; Asakawa et al., 2003). The Malaysian *Chandonanthus hirtellus* (F. Weber) Mitt. elaborates limonene (3) (Asakawa et al., 1991). The New Zealand species *Plagiochila fasciculata* Lindenb. contained α -terpinene (4), carvacrol (5), and thymol (6). The latter two compounds have also been detected in *Trichocolea lanata* (Hook.) Nees (Asakawa et al., 1996). Reinvestigation of the ether extract of *P. stephensoniana* showed that it biosynthesized a relatively high amount of α -terpinene (4) (Asakawa et al., 1996). β -Myrcene (7) together with bibenzyl derivatives are the main components detected in the New Zealand *F. falciloba* (Asakawa et al., 2003).

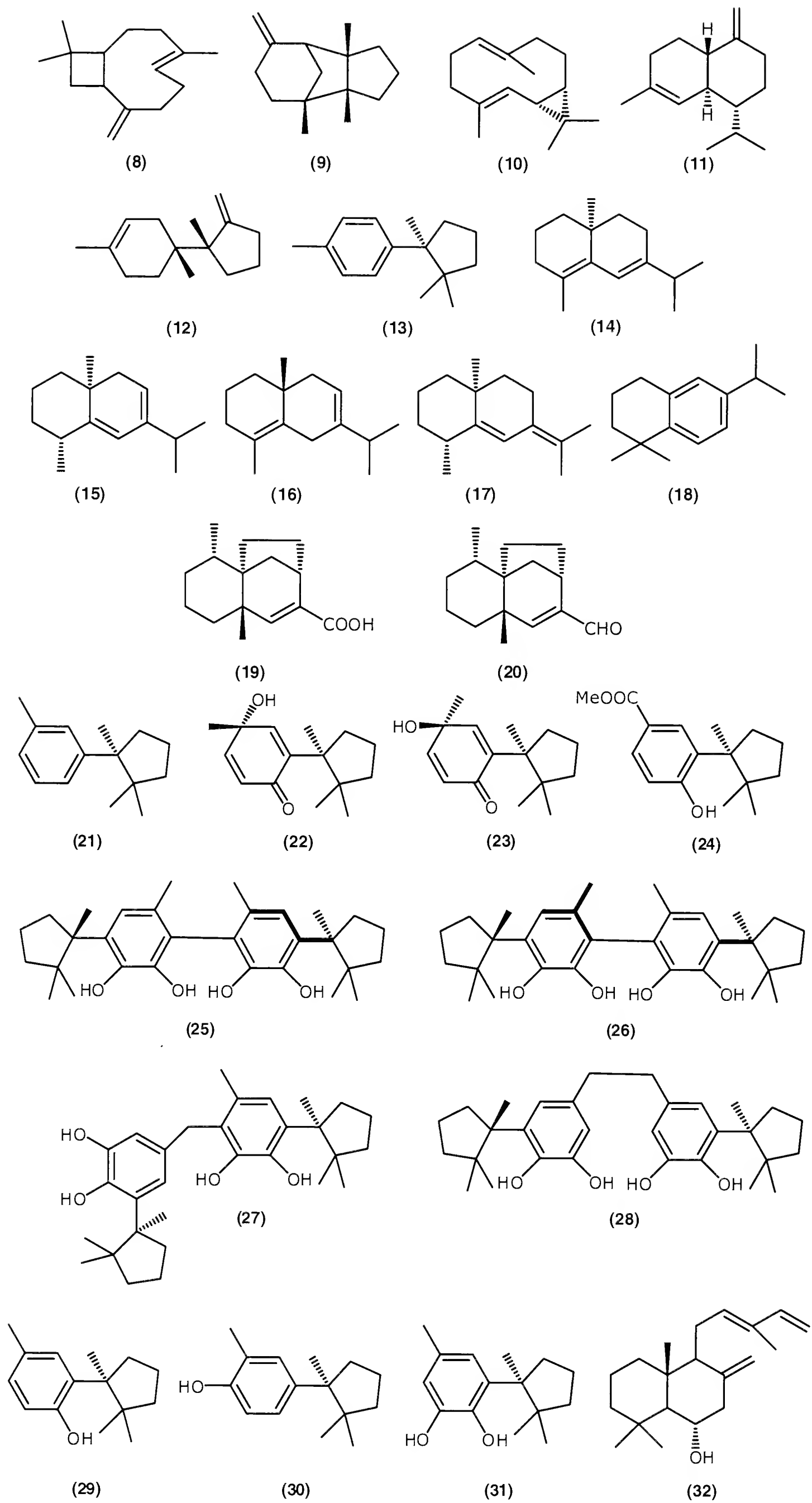
Sesquiterpenoids

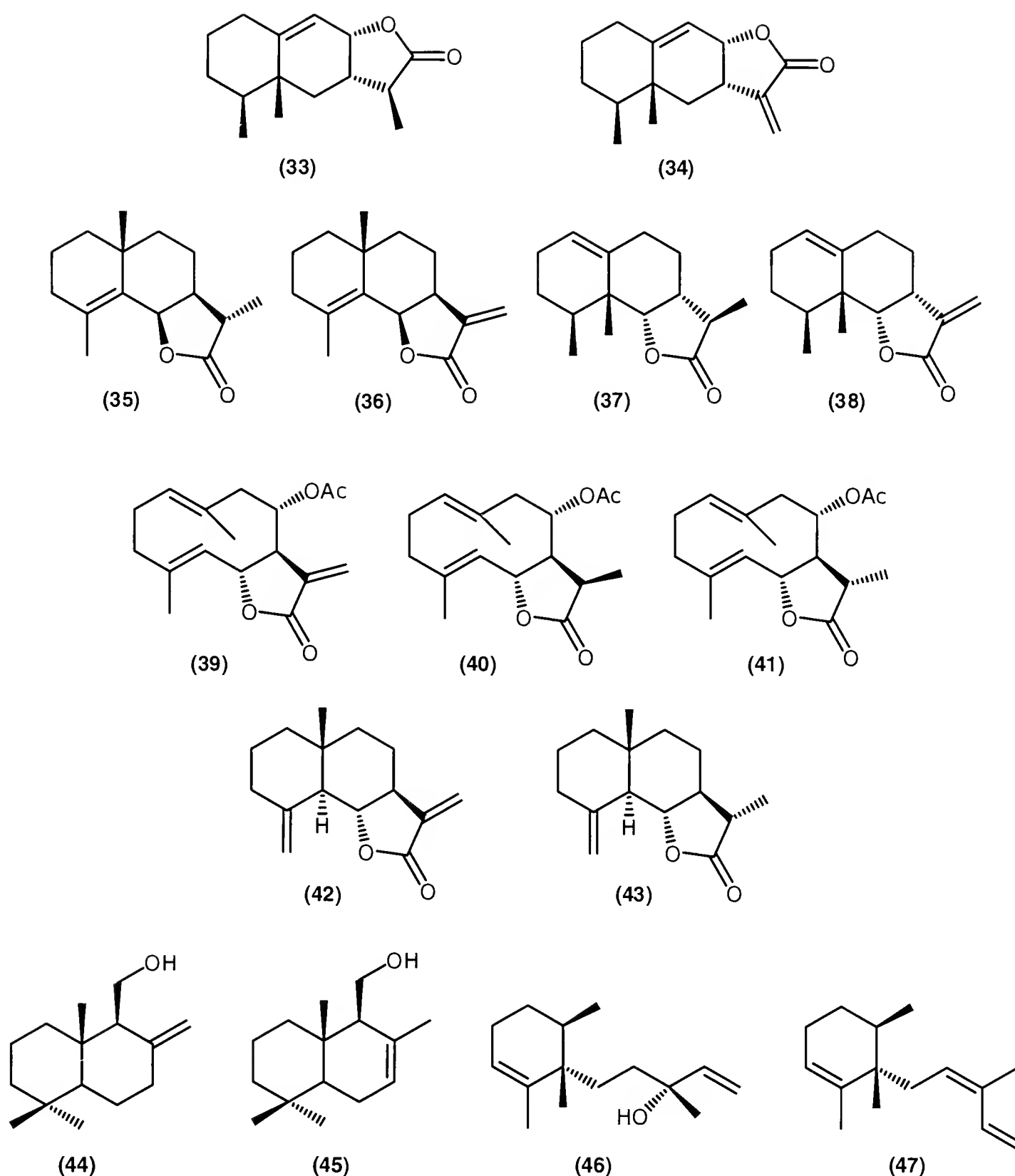
Sesquiterpene structures present several acyclic, mono-, bi-, and tricyclic systems, including many unique combinations. The oil bodies of most southern hemispheric liverworts contain all of the mentioned sesquiterpenoids. Among sesquiterpenoids, liverworts produce mainly sesquiterpene hydrocarbons. Asakawa et al. (2003) reported that β -caryophyllene (8), β -barbatene (9), and bicyclogermacrene (10) are prevalent throughout *Frullania*. Among 24 investigated New Zealand, Australian, and South American *Frullania* species, these three compounds were

detected in 17 species. A large amount of bicyclogermacrene (10) together with unidentified sesquiterpene alcohol were also found in the Ecuadorian *Noteroclada confluens* Taylor ex Hook. f. & Wilson (Ludwiczuk et al., 2008). *Schistochila aligera* (Nees & Blume) J.B. Jack & Steph. from Malaysia elaborates bicyclogermacrene (10) and γ -cadinene (11) as the major components, while *Lepidozia borneensis* Steph. produces high amounts of bazzanene (12) and also cuparene (13) (Asakawa et al., 1991). The latter two compounds are widespread in *Bazzania* species belonging to the same Lepidoziaceae family as those of *Lepidozia*. Eudesmane-type sesquiterpene hydrocarbons, δ -selinene (14), cascarilladiene (15), selina-4,7-diene (16), and eudesma-5,7(11)-diene (17) have been detected in *Symphyogyna brasiliensis* Nees & Mont. from Ecuador (Ludwiczuk et al., 2008). *Archilejeunea olivacea* (Hook. f. & Taylor) Steph. collected in New Zealand produces olivacene (18), a new naturally occurring sesquiterpene hydrocarbon (Toyota et al., 1997b; Asakawa, 2001).

A new tricyclic sesquiterpenoid, nudeonic acid (19) has been isolated from *Mylia nuda* Inoue & B. Y. Yang, a species endemic to Taiwan. This species also contains the unstable nudenal (20) (Liu et al., 1996; Asakawa, 2001).

The New Zealand *Dendromastigophora flagellifera* produces herbertane (= isocuparane) sesquiterpenoids of which herbertenone A (22) and B (23) are the major components (Asakawa et al., 1996, 2007). Such sesquiterpenoids and also herbertane dimers, named mastigophorenes A (25), B (26), C (27), and D (28), have been detected in the East Malaysian *Mastigophora diclados* (Brid. ex F. Weber) Nees (Asakawa et al., 1991). The main compound of the Malagasy *M. diclados* is herbertene (21). The other herbertane

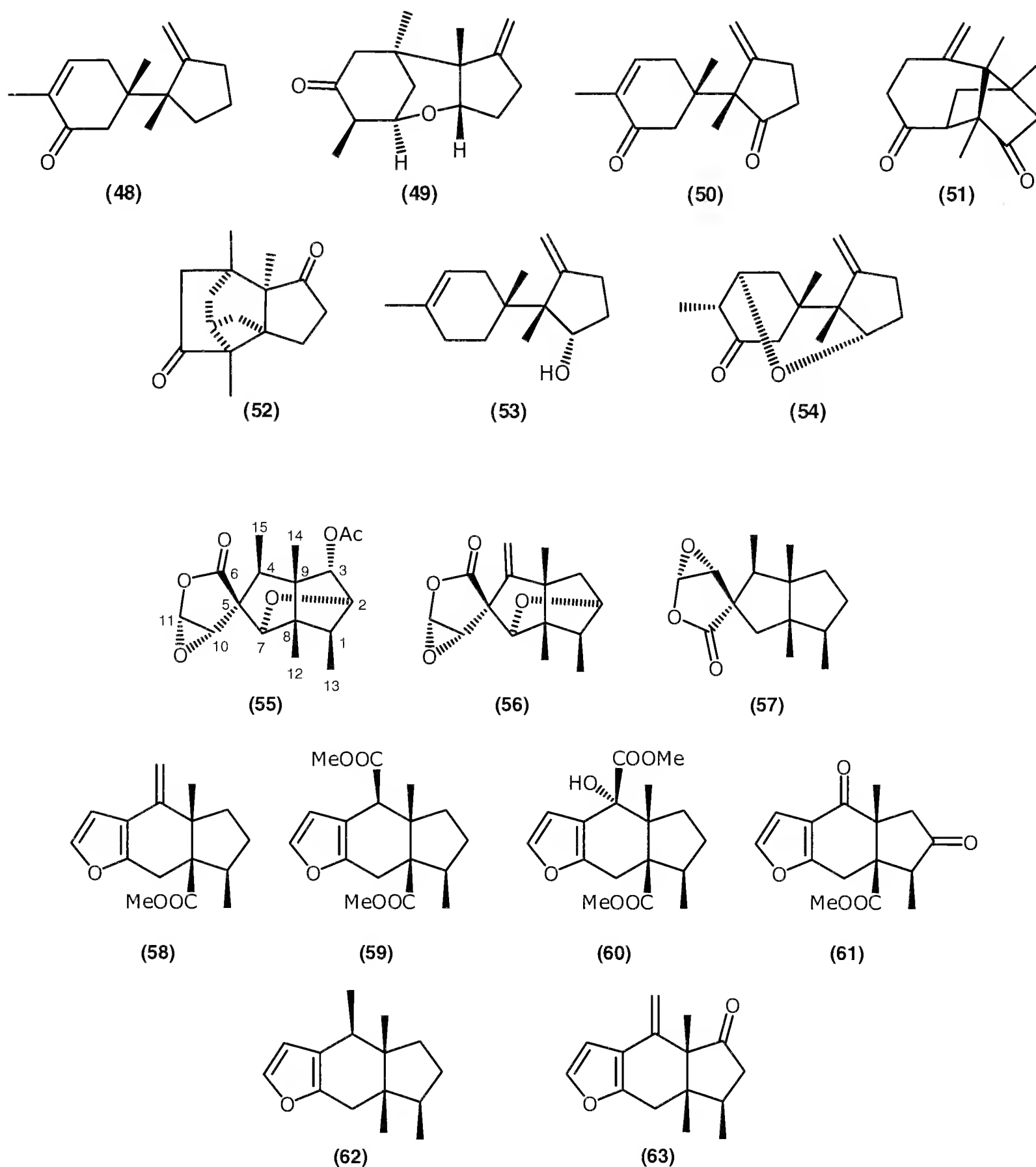




monomers and dimers together with the new compound, mastigophoric acid methyl ester (**24**), have also been isolated (Harinantenaina & Asakawa, 2004a, 2007b). These results indicate that *D. flagellifera* is chemically quite similar to the *Mastigophora*. Both liverworts belong to the Lepicoleaceae family. Asakawa (1995, 2004) indicated that the Lepicoleaceae are chemically almost equal to the Herbertaceae and that the two families might originate from a common ancestor. Two investigated Ecuadorian *Herbertus* species—*H. subdentatus* (Steph.) Fulford and *H. acanthelius* Spruce—produce herbertane-type sesquiterpenoids. In both species, (-)- α -herbertenol (**29**) has been detected, and additionally, from former species, (-)- β -herbertenol (**30**) and (-)-herbertenediol (**31**) have been isolated (Nagashima et al., 1991a). The New

Zealand *Herbertus alpinus* (Steph.) E.A. Hodgs. is chemically quite distinct from the Herbertaceae family since it biosynthesizes neither herbertanes nor herbertane dimers but instead labdane diterpenoid, 8(17),12,14-labdatrien-6 α -ol (**32**) as its major component (Asakawa et al., 1996). Thus, there are two chemical types of *Herbertus*.

Frullania is a very large and complex genus with over 1,000 binomials, which are rich sources of sesquiterpenoids, especially sesquiterpene lactones, diterpenoids, and bibenzyl derivatives (Asakawa et al., 2003; Asakawa, 2004). The sesquiterpene lactones, dihydroeremofrullanolide (**33**) and eremofrullanolide (**34**), are significant chemical constituents of the New Zealand *Frullania media* (E. A. Hodgs.) S. Hatt. In other two *Frullania* species (*F. congesta* Gottsche, Lindenb. & Nees and *F. incumbens* Mitt. in Hook.



f.), dihydrofrullanolide (35) and frullanolide (36) were detected. *Frullania magellanica* F. Weber & Nees elaborated only dihydrofrullanolide (35). It is noteworthy that *F. probosciphora* Taylor biosynthesizes both eremophilanolides (dihydro-eremofrullanolide [33] and eremofrullanolide [34]) and eudesmanolides (frullanolide [36]) (Asakawa et al., 2003). Both eremophilane-type and eudesmane-type sesquiterpene lactones have also been detected in the Argentinean *F. brasiliensis* Raddi. From this liverwort species, 5-epidilatanolides A (37) and B (38) and also frullanolide (36) and dihydrofrullanolide (35) have been isolated (Bardón et al., 2002). *Frullania serrata* Gottsche in Gottsche, Lindenb. & Nees

collected in Malaysia produces germacranolides, tulipinolide (39), (11*R*)-dihydrotulipinolide (40), and (11*S*)-dihydrotulipinonide (41) (Asakawa et al., 1991). Tulipinolide (39) and its cyclized compounds are the chemical markers of the thalloid liverwort *Wiesnerella denudata* (Mitt.) Steph. (Asakawa, 1982a, 1995). This is the first isolation of 39 and its dihydroderivatives (40 and 41) from Jungermanniales. The investigated New Zealand *Frullania chevalieri* (R. M. Schust.) R. M. Schust. also elaborates sesquiterpene lactones. Eudesmanolides, β -cyclocostunolide (42) and dihydro- β -cyclocostunolide (43) have been detected in this species (Asakawa et al., 2003). It is significant because the status of this species

remained controversial for a very long time. Von Konrat et al. (2006) reported that chemical and morphological evidence indicates very strongly that *Frullania chevalieri* (not *Schusterella*) and its allies should indeed be retained in the genus *Frullania*.

The New Zealand *F. monocera* (Taylor) Gottsche, Lindenb. & Nees is very characteristic since it produces a drimane-type sesquiterpene alcohol, albicanol (**44**), as the major component, while the presence of drimenol (**45**) in the Australian *F. clavata* (Hook. f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees was confirmed. The New Zealand *F. deplanata* Mitt. biosynthesizes striatene-type sesquiterpene alcohol, striatol (**46**); however, in the Australian specimen, **46** was not detected (Asakawa et al., 2003). Striatene (**47**), a sesquiterpene hydrocarbon which is one of the valuable chemical markers of the Lejeuneaceae family, was detected in *F. incumbens* from New Zealand (Asakawa et al., 1996, 2003).

From the ether extract of an unidentified New Zealand *Frullania* species, three new bazzanene-type sesquiterpenoids, named bazzanenone A (**48**), B (**49**), and C (**50**), and modified bazzanene-type sesquiterpene diketone, bazzanenone D (**51**), have been isolated (Asakawa et al., 1996). Bazzanane sesquiterpenoids have also been detected in *F. squarrosula* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees: bazzanenone C (**50**), D (**51**), and two other compounds (**52**, **53**) and in *F. falciloba*: 2-oxobazzanene (= bazzanenone A) (**48**) and bazzanenoxide (**54**) (Nagashima et al., 2006a; Asakawa et al., 2008). The presence of bazzananes in *Frullania* is very rare; these compounds are distributed in Lepidoziaceae, particularly in *Bazzania* species (Asakawa, 1982a, 1995).

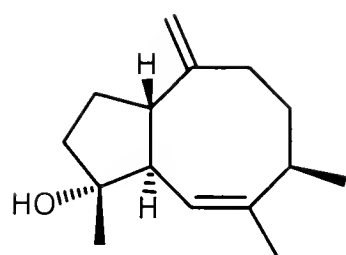
The pinguisane-type sesquiterpenoids have been detected in Marchantiophyta, especially in the Lejeuneaceae, Trichocoleaceae, Ptilidiaceae, Porellaceae, and Aneuraceae. However, these types of compounds have not been found in any other organisms. The investigation of the chemical constituents of the Bolivian *Frullanoides densifolia* Raddi belonging to the Lejeuneaceae family led to isolation of new pinguisane-type sesquiterpenoids, spirodensifolin A (**55**) and B (**56**). It is very interesting that ptychanolide (**57**) also was found in this liverwort, although the stereochemistry at C-5 was different from those of **55** and **56** (Tori et al., 1992). The Panamanian *Bryopteris*

filicina (Sw.) Nees (Lejeuneaceae) produces pinguisane-type sesquiterpenoids as its major components. Bryopterins A–D (**58–61**) have been isolated from this liverwort species (Nagashima et al., 1994a). Some *Plagiochila* species are very distinct from the rest and belong to chemotype VII (pinguisane-type) of the Plagiochilaceae (Asakawa, 2004). Deoxopinguisone (**62**) was found in the Peruvian *Plagiochila rosariensis* Steph. (Asakawa & Inoue, 1987b). The same compound was isolated from the Ecuadorian *P. alternans* Lindenb. & Gottsche as the major component (Nagashima et al., 1991a). From the New Zealand *P. retrospectans* (Nees) Nees dehydropinguisone (**63**) was isolated (Nagashima et al., 1994b).

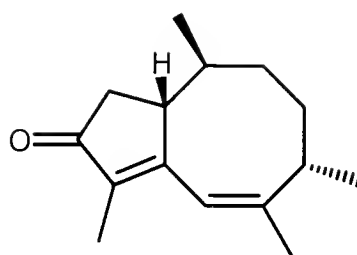
Dumortanol (**64**) and other dumortane- (**65**, **66**) and nordumortane-type (**67**) compounds have been isolated from the Argentinean *Dumortiera hirsuta* (Sw.) Nees (Toyota et al., 1997a; Bardón et al., 1999a). It is noteworthy that the Japanese *D. hirsuta* does not contain any dumortane-type sesquiterpenoids (Asakawa, 2001). Another investigated Argentine liverwort, *Plagiochasma rupestre* (G. Forst.) Steph., produced rupestrenol (**68**), a new cadinane-type sesquiterpene alcohol (Bardón et al., 1999b).

The *Porella* species are divided into two groups, pungent and nonpungent. The former contains the strongly pungent sesquiterpene dialdehyde, polygodial, as the major component (Asakawa, 2004; Bovi Mitre et al., 2004). The leafy liverwort *Porella swartziana* (F. Weber) Trevis. belongs to the nonpungent group. This liverwort produces africane-type sesquiterpenoids. Analysis of this Colombian species gave five africane-type sesquiterpenoids: caespitenone [**69**], swartzianins A [**70**], B [**71**], C [**72**], and D [**73**], two secoafricans (secoswartzianins A [**74**] and B [**75**]), and one norsecoafrikan-type sesquiterpenoid (norsecoawartzianin [**76**]) (Tori et al., 1993, 1996). From the Argentine collection of the same species, four other new africane-type sesquiterpenoids (**77–80**) have been isolated (Bovi Mitre et al., 2004).

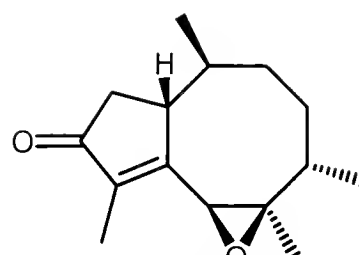
The genus *Bazzania* produces a wide range of sesquiterpenoids. The sesquiterpenoids that have been detected are of bazzanene, cuparane, barbatene, aromadendrene, bicyclogermacrene, calamenane, drimane, chamigrane, pinguisane, myltaylane, and cyclomyltaylane types (Asakawa, 1995, 2004). Myltaylanes and cyclomyltaylanes are very rare sesquiterpenoids found only in



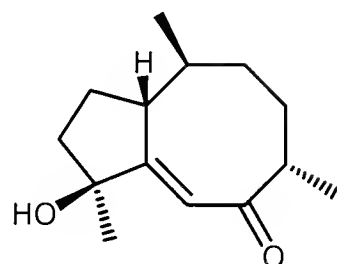
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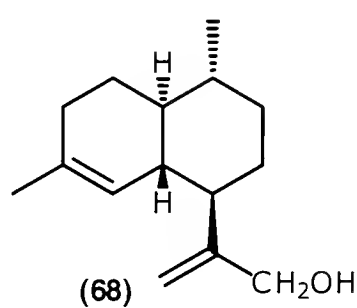
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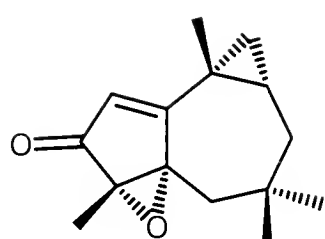
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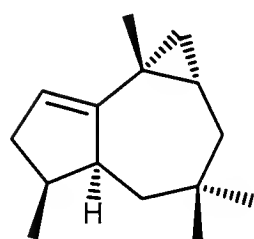
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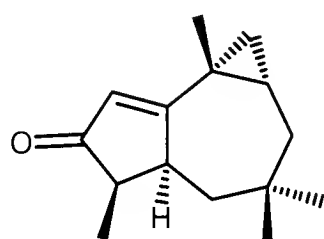
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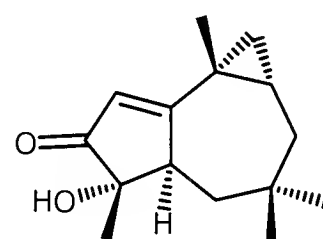
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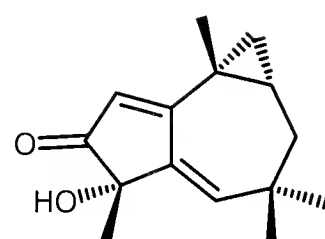
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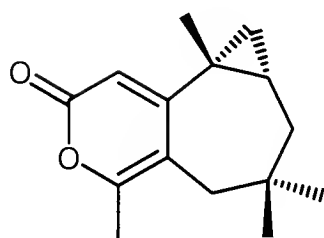
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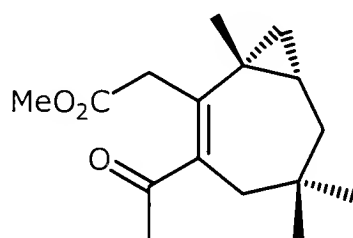
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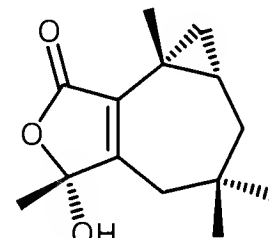
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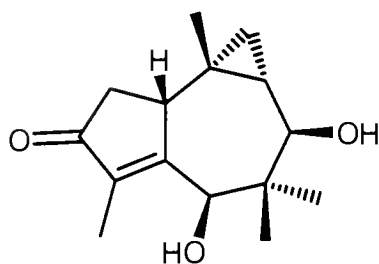
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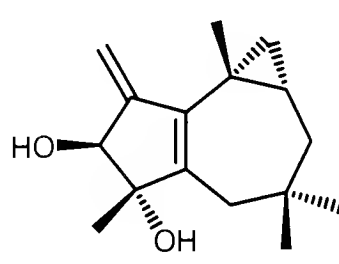
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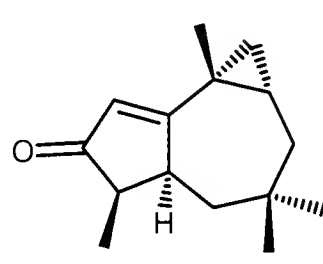
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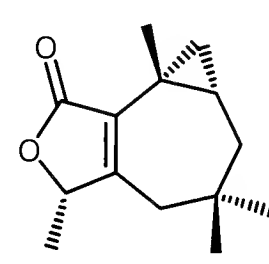
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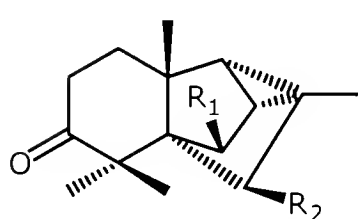
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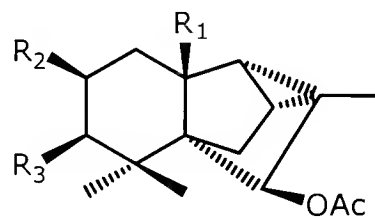
(80)



(81) $R_1 = \text{OCOCH}_3$; $R_2 = \text{OCOCH}_3$

(82) $R_1 = \text{OH}$; $R_2 = \text{OCOCH}_3$

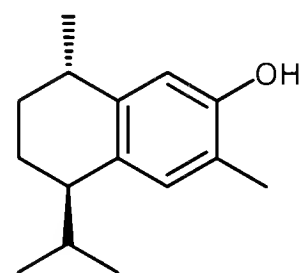
(83) $R_1 = \text{OH}$; $R_2 = \text{OH}$



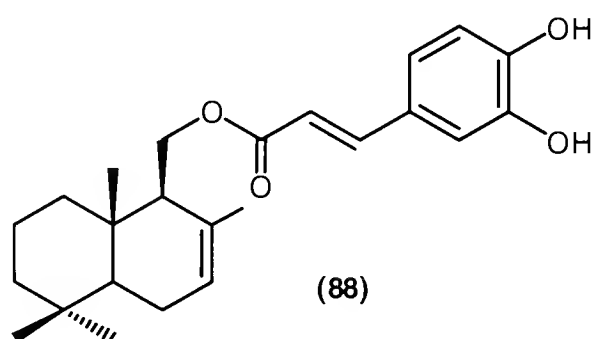
(84) $R_1 = \text{CH}_3$; $R_2 = \text{OH}$; $R_3 = \text{OCOCH}_3$

(85) $R_1 = \text{CH}_2\text{OCOCH}_3$; $R_2 = \text{OH}$; $R_3 = \text{OCOCH}_3$

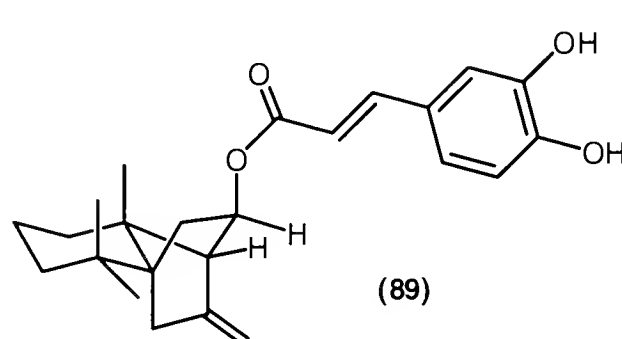
(86) $R_1 = \text{CH}_2\text{OCOCH}_3$; $R_2 = \text{OCOCH}_3$; $R_3 = \text{OH}$



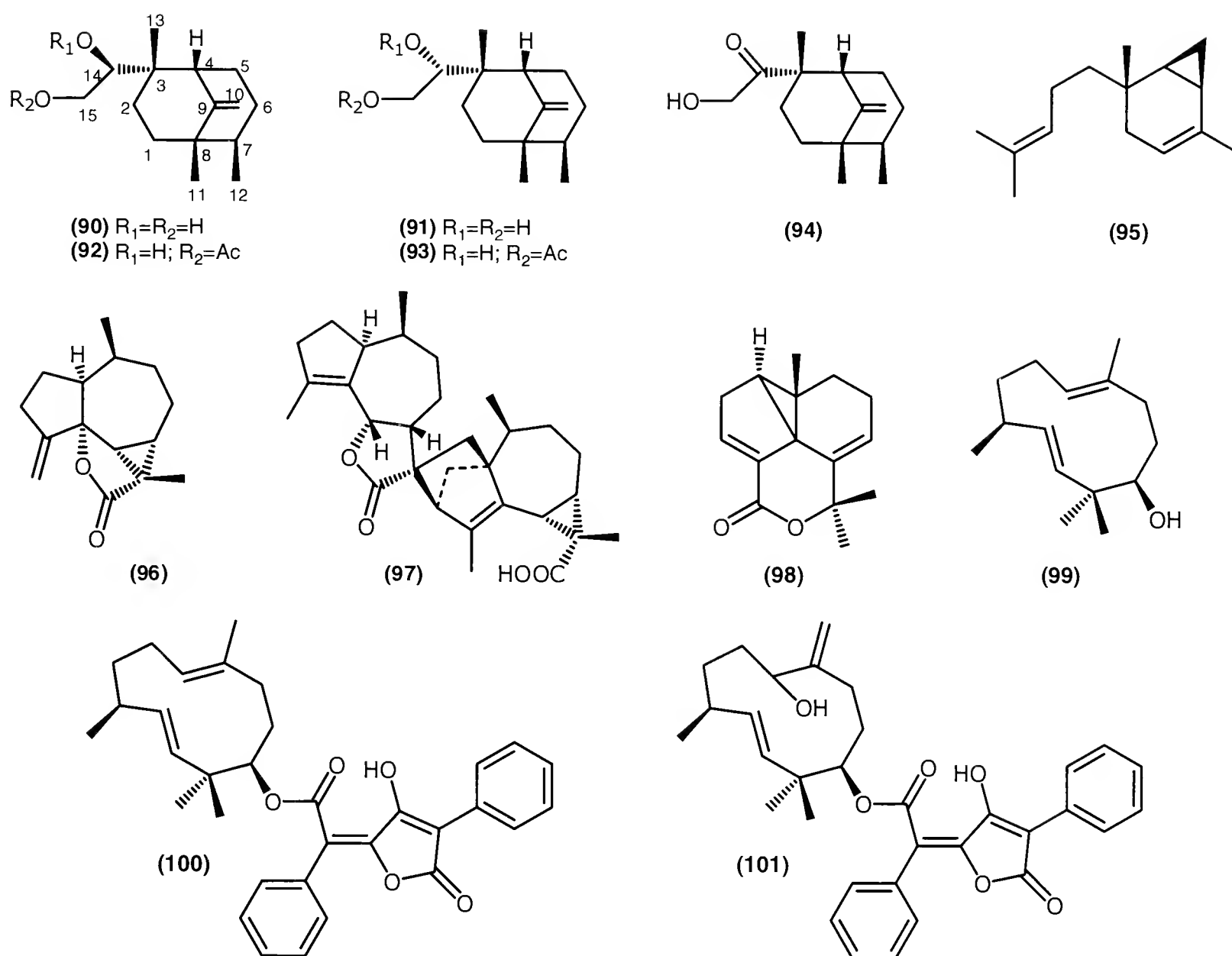
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(88)



(89)

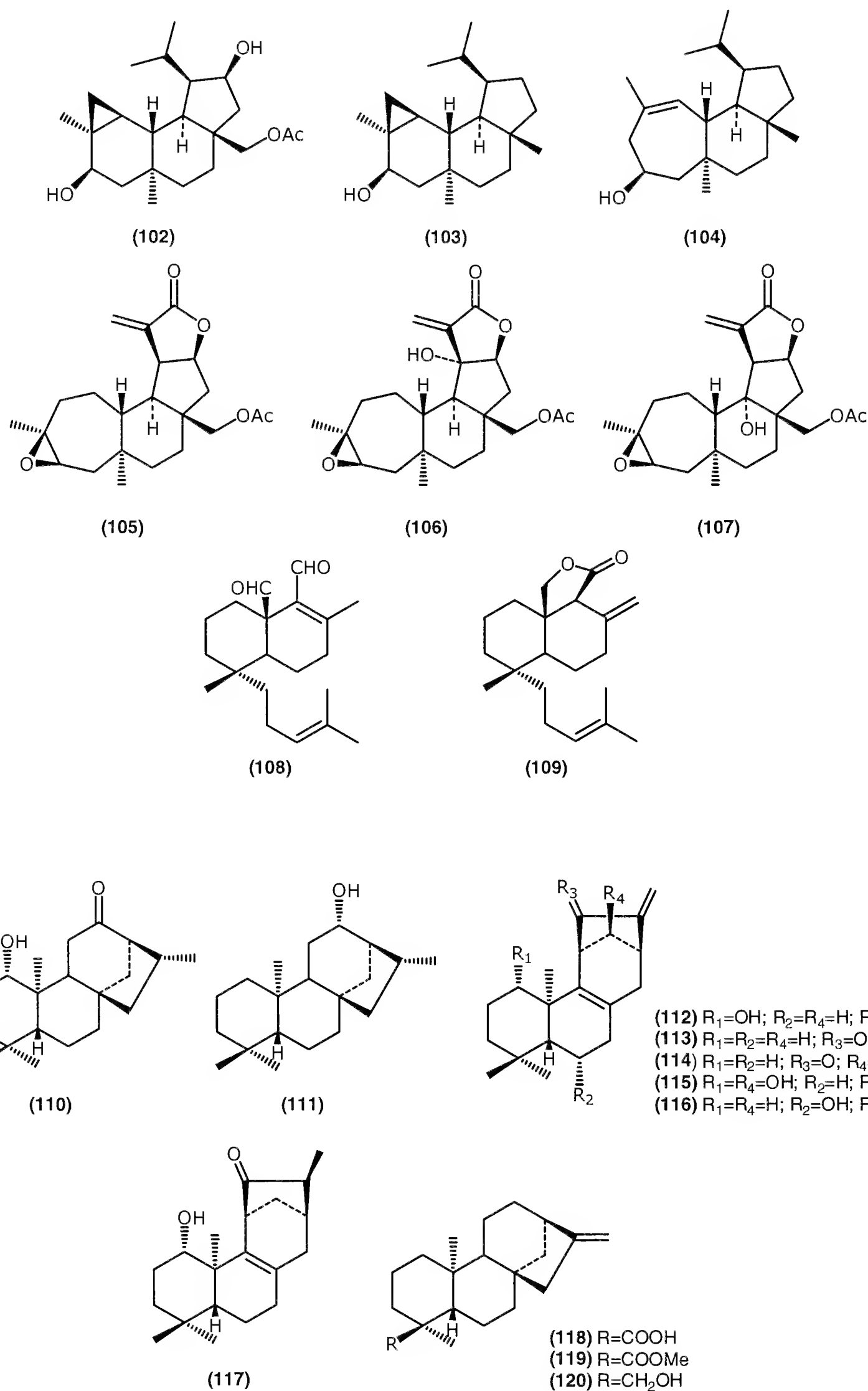


liverworts from the genera *Mylia*, *Bazzania*, *Reboulia*, and *Mannia*. In the investigated Malagasy *Bazzania madagassa* (Steph.) S. W. Arnell, six new cyclomyltaylane-type sesquiterpenoids (**81–86**) have been isolated (Harinantenaina et al., 2006a). *Bazzania decrescens* (Lehm. & Lindenb.) Trevis. is a species morphologically close to *B. madagassa*. However, neither myltaylanes nor cyclomyltaylanes have been detected in *B. decrescens*. This liverwort contains drimenol (**45**) and drimenyl caffeate (**88**), together with cuparane-type sesquiterpenoids (Harinantenaina et al., 2005). The third of the investigated Malagasy *Bazzania* species, *Bazzania nitida* (F. Weber) Grolle, biosynthesizes (+)-(1*S*,4*R*)-7-hydroxycalamenene (**87**) and myltayl-4(12)-ene-2-caffeate (**89**) (Harinantenaina & Asakawa, 2007a). Interestingly, sesquiterpene caffeates (**88**, **89**), which have been isolated from *B. decrescens* and *B. nitida*, have been found only in *Bazzania* species (Asakawa, 1995, 2004).

The Malaysian liverwort *Cheilolejeunea trifaria* (Reinw., Blume & Nees) Mizut. belonging to the Lejeuneaceae was chemically analyzed to give five new bicyclic nonisoprenoid sesquiterpene

alcohols, named trifarienols A–E (**90–94**). These unique sesquiterpenoids might be biosynthesized from striatane-type sesquiterpenoids, which are also present in this liverwort (Hashimoto et al., 1995). This is the first report of the isolation of trifarane-type sesquiterpenoids from a natural source, possessing *S* configuration at C-3. It is interesting to note that the marine sponge *Dysidea fragilis* Montagu biosynthesizes a trifarane with *R* configuration at C-3 (Schulte et al., 1980). *Plagiochila terebrans* Nees & Mont. collected in Madagascar is the second liverwort found to contain trifarienol B (**91**) (Harinantenaina & Asakawa, 2007b).

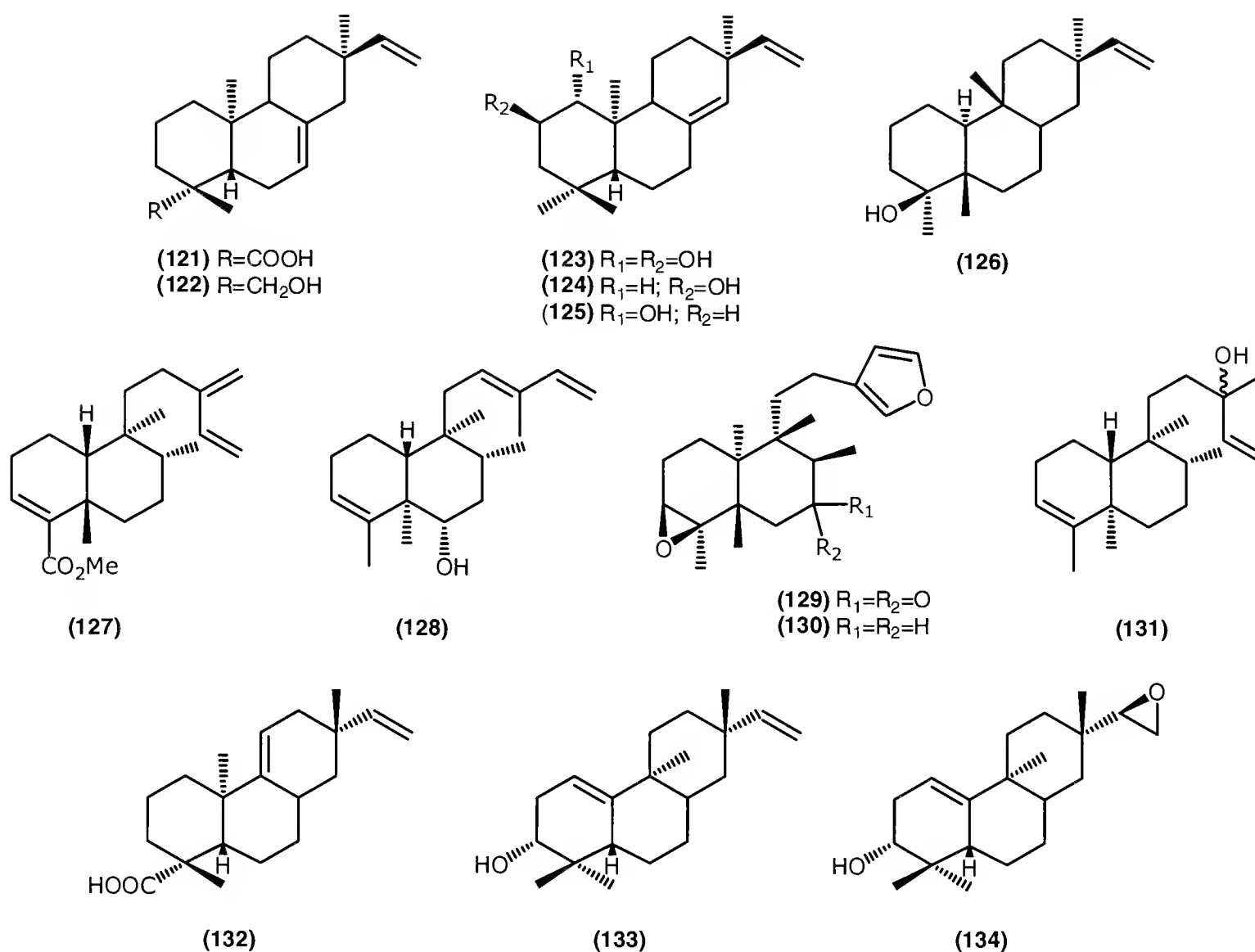
A new aromadendrane-type sesquiterpenoid, 4(15)-aromadendren-12,5 α -olide (**96**), and aromadendrane-guaianolide dimer (**97**) have been isolated from the New Zealand *Chiloscyphus subporosus* (Mitt.) J. J. Engel & R. M. Schust. (Nagashima et al., 2004a). The presence of aromadendrane-guaianolide dimer is the first record in liverworts. The other New Zealand liverwort species, *Lepidozia spinosissima* (Hook. f. & Taylor) Mitt., produces cyclogorgonane-type sesquiterpenoids. The structure of 1,5-cyclo-3,6-



gorgonadien-15,11-olide (**98**) was established by the extensive NMR techniques and chemical reactions (Nagashima et al., 2005b).

Three new sesquiterpenes have been isolated from the New Zealand *Tylimanthus tenellus* (Taylor ex Lehm.) Mitt. The structures of the new compounds were shown to be humulane-type

sesquiterpene alcohol, 1,6-humuladien-10-ol (**99**), and two esters (**100**, **101**) (Toyota et al., 2004). The fractionation of the ether extract of *Marchantia chenopoda* L. collected in Venezuela afforded a new sesquiterpene, chenopodene (**95**), which belongs to a new rearranged sesquicaran-type sesquiterpenoid (Tori et al., 1994a).



Diterpenoids

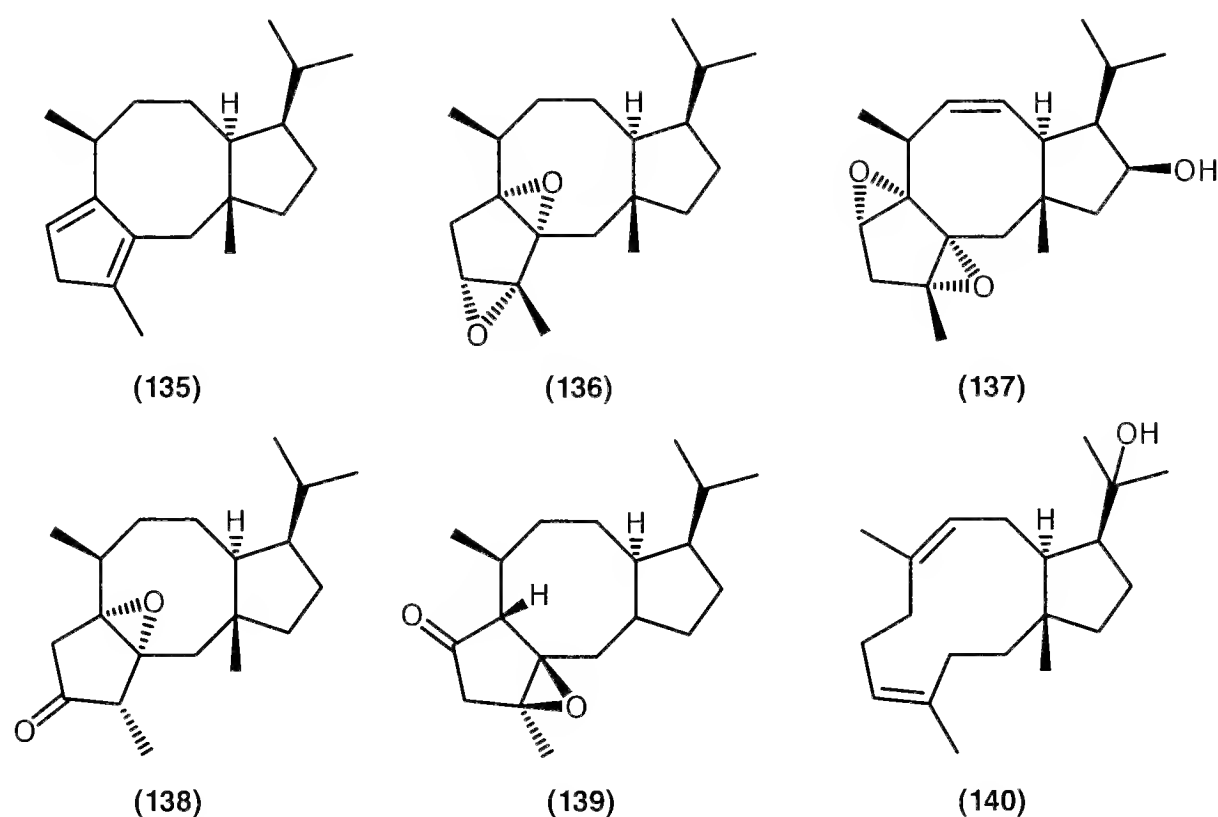
Liverworts are also rich sources of a number of different skeletal diterpenoids. Five unique diterpenoids have been isolated from the New Zealand *Jamesoniella tasmanica* (Hook. f. & Taylor) Steph., which belongs to the Lophoziaceae. They were shown to be 13-*epi*-neoverrucosane (**102** and **103**) and highly oxygenated 13-*epi*-neohomoverrucosane-type diterpenoids (**105–107**) (Toyota et al., 1996; Asakawa, 2001). Verrucosane-type (=cyathane-type) diterpenoids are also present in *Schistochila nobilis* (Hook.) Trevis. In this beautiful liverwort, distributed only in New Zealand, two diterpene alcohols, 13-*epi*-homoverrucosan-5 β -ol (**104**) and 13-*epi*-neoverrucosan-5 β -ol (**103**), have been detected (Asakawa et al., 1988b). Compound **102** has also been isolated from the New Zealand *Plagiochila stephensoniana* (Fukuyama et al., 1988).

Paraschistochila pinnatifolia (Hook.) R. M. Schust. collected in New Zealand elaborates sacculatane-type diterpenoids (**108**, **109**) along with two kauranes (**110**, **111**) (Asakawa et al., 2007). Perrottetianal A (**108**) is the main component detected in the New Zealand *Porella elegantula* (Mont.) E. A. Hodgs. (Asakawa & Campbell,

1982). Among the *Porella* species examined so far, *P. elegantula* is chemically quite similar to the Japanese *P. perrottetiana* (Mont.) Trevis. (Asakawa, 1995).

The liverworts belonging to the genus *Jungermannia* are rich sources of diterpenoids, such as clerodane, kaurane, pimarane, and labdane types. An unidentified New Zealand *Jungermannia* species contains kaurane-type diterpenoids as the main components. The isolation of jungermannenones A-E (**112–116**) and 16 α ,17-dihydrojungermannenone A (**117**) from this species was the first report of the presence of these compounds in liverworts (Nagashima et al., 2003b, 2005a). The following *ent*-kauranes, *ent*-16-kauren-19-oic acid (**118**), *ent*-methyl-16-kauren-19-oate (**119**), and *ent*-16-kauren-19-ol (**120**) and two *ent*-isopimaranes, oblongifolic acid (**121**) and *ent*-isopimara-7(8),15-dien-19-ol (**122**), have been isolated from the New Zealand *Jamesoniella kirkii* Steph. (Nagashima et al., 2006b). These data are the first description of chemical components of *J. kirkii*.

The fractionation of the ether extract of the New Zealand *Trichocolea mollissima* (Hook. f. & Taylor) Gottsche gave two new *ent*-isopimarane-type diterpenoids, (1*R*,2*R*)-*ent*-1,2-dihydroxyisopimara-8(14),15-diene (**123**) and



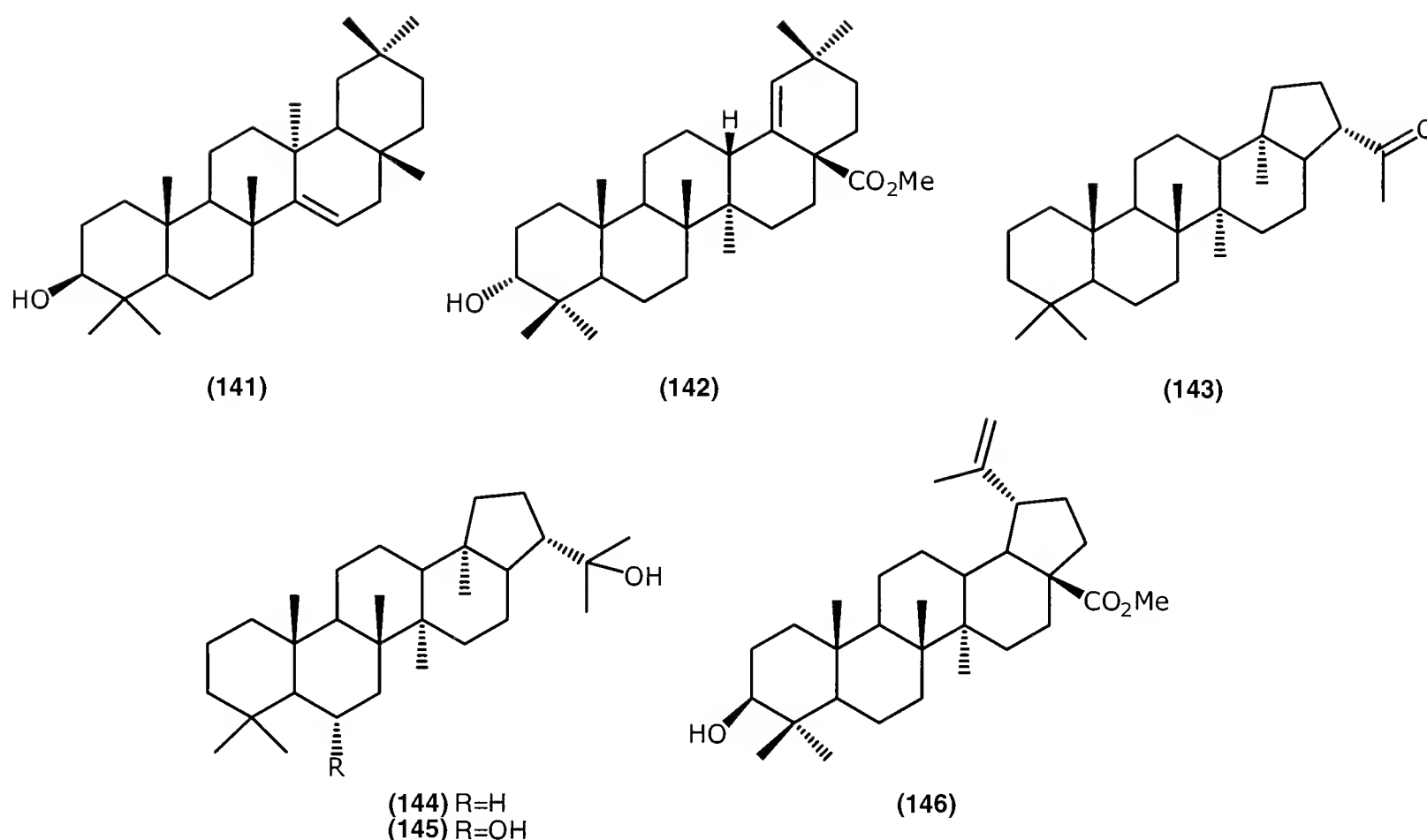
(2*R*)-*ent*-2-hydroxyisopimara-8(14),15-diene (**124**), along with a known 1 α -hydroxy-*ent*-sandara-copimara-8(14),15-diene (**125**) (Nagashima et al., 2003a). Pimarane-type diterpenoids are also present in the Malaysian *Schistochila aligera*. From the methanol extract of this liverwort, a new rearranged pimarane-type diterpene alcohol (**126**) together with a new clerodane-type diterpene, *cis*-clerod-3,13(16),14-trien-19-oic acid methyl ester (**127**), have been isolated (Nagashima et al., 1991b). A clerodane-type diterpenoid, 6 α -hydroxy-3,12*E*,14-clerodatriene (**128**), has also been isolated from the New Zealand *Heteroscyphus billardi* (Schwägr.) Schiffn. (Nagashima et al., 2004b).

A new clerodane-type diterpenoid named thysaspathone (**129**) together with the known 3 β ,4 β :15,16-diepoxy-13(16),14-clerodadiene (**130**) were isolated from the liverwort *Thysananthus spathulistipus* (Reinw.) Lindenb. (Lejeuneaceae) collected in Madagascar (Harinantenaina et al., 2006b; Harinantenaina & Asakawa, 2007b). The distribution of clerodane-type diterpenoids among Lejeuneaceae is very rare. The only example of the isolation of (-)-kolavelool (**131**) has been reported for the Ecuadorian *Macrolejeunea pallescens* (Mitt.) Schiffn. (Nagashima et al., 1991a).

Two new *ent*-rosane-type diterpenoids, 1(10),15-rosadien-3 α -ol (**133**) and (3*R*,15*R*)-*ent*-15,16-epoxy-1(10)-rosen-3-ol (**134**), have been isolated from the ether extract of *Plagiochila deltoidea* Lindenb. collected in New Zealand. From this

Plagiochila species, *ent*-pimarane-type diterpenoid, acanthonic acid (**132**), has also been isolated (Nagashima et al., 2004b). This is the first report of isolation of *ent*-rosane- and *ent*-pimarane-type diterpenoids from a *Plagiochila* species.

Occurrence of fusicoccane-type diterpenoids in nature is rare. Several fusicoccanes have been isolated from the liverworts belonging to the Lophoziaceae, Pleuroziaceae, Plagiochilaceae, Lejeuneaceae, Riccardiaceae, and Pallaviciniaceae (Asakawa, 1995). 2(3),5(6)-Fusicoccadiene (**135**) and fusicogigantepoxide (**136**) have been detected in the Australian *Frullania falciloba*. The presence of the latter compound was also confirmed in the New Zealand material. Both compounds have also been found in the New Zealand *F. squarrosula* and *F. patula* Mitt. in Hook. f., while fusicoccanes as well as bibenzyl derivatives are the main components of the latter species (Asakawa et al., 2003). Fusicogigantepoxide (**136**) mentioned previously was detected in the Panamanian liverwort *Bryopteris filicina* belonging to the Lejeuneaceae (Nagashima et al., 1994a). From the Venezuelan liverwort *Plagiochila corrugata* (Nees) Nees & Mont., a new fusicoccane-type diterpene alcohol, fusicorruगतol (**137**), has been isolated (Tori et al., 1994b). Fusicogigantone A (**138**) and B (**139**) and fusicogigantepoxide (**136**) together with dolabellane-type diterpenoid 18-hydroxy-4,8-dolabelladiene (**140**) are biosynthesized in *Pleurozia gigantea* (F. Weber) Lindb. collected in East Malaysia (Asakawa et al., 1990). This is the first record of the co-occurrence of the biogenetically correlated



dolabellane- and fusicoccane-type diterpenoids in the plant kingdom.

Triterpenoids

Frullania fugax (Hook. f. & Taylor) Gottsche, Lindenb. & Nees from New Zealand produces a triterpene alcohol, taraxerol (141), as the major component (88%) (Asakawa et al., 2003). It was the first instance of detecting such a large amount of a triterpenoid in a species of Marchantiophyta, although methyl 3 α -hydroxy-18-oleanen-28-oate (142) has been found in an unidentified *Frullania* species collected in Venezuela (Asakawa, 1995).

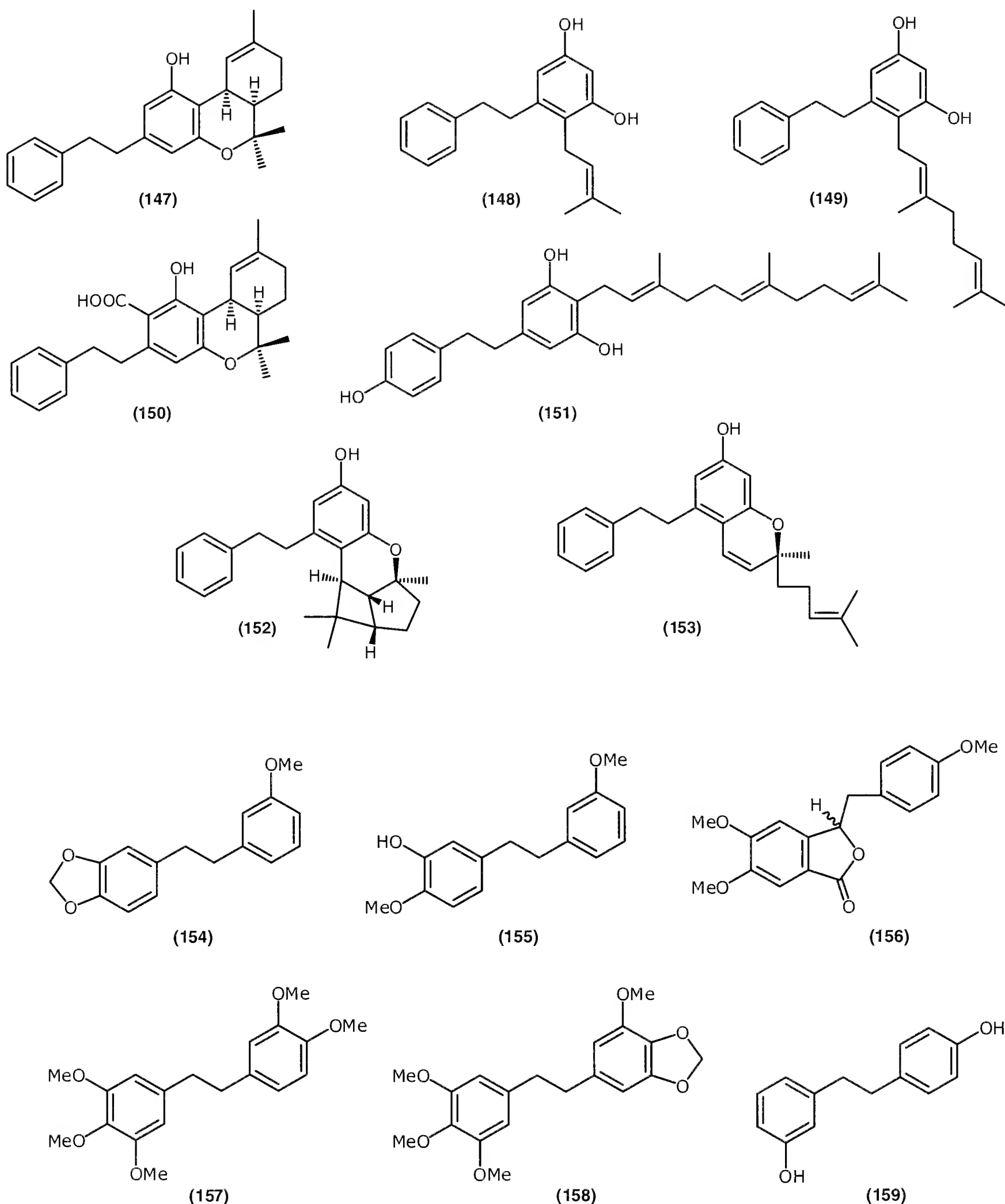
Hopanoids are triterpenes widely distributed among bacteria and cyanobacteria and have been found in few genera of liverworts, such as in the Japanese *Conocephalum japonicum* (Thunb.) Grolle (Toyota & Asakawa, 1993). From *Plagiochasma rupestre* collected in Argentina, three hopanoids, adianton (143), diplopterol (144), and zeorin (145), have been isolated (Bardón et al., 1999b). Zeorin (145) has also been found in the Japanese *P. pterospermum* C. Massal. and *P. japonicum* (Steph.) C. Massal. (Hashimoto et al., 1998; Lahlou et al., 2000). Thus, this triterpene alcohol is one of the chemical markers of the genus *Plagiochasma*. Zeorin (145) has also been isolated from the Argentine *Frullania brasiliensis*

(Bardón et al., 2002). Lupane-type triterpenoid, betulinic acid methyl ester (146), has been detected in the New Zealand *Plagiochila deltoidea* (Nagashima et al., 2004b).

Aromatic Compounds

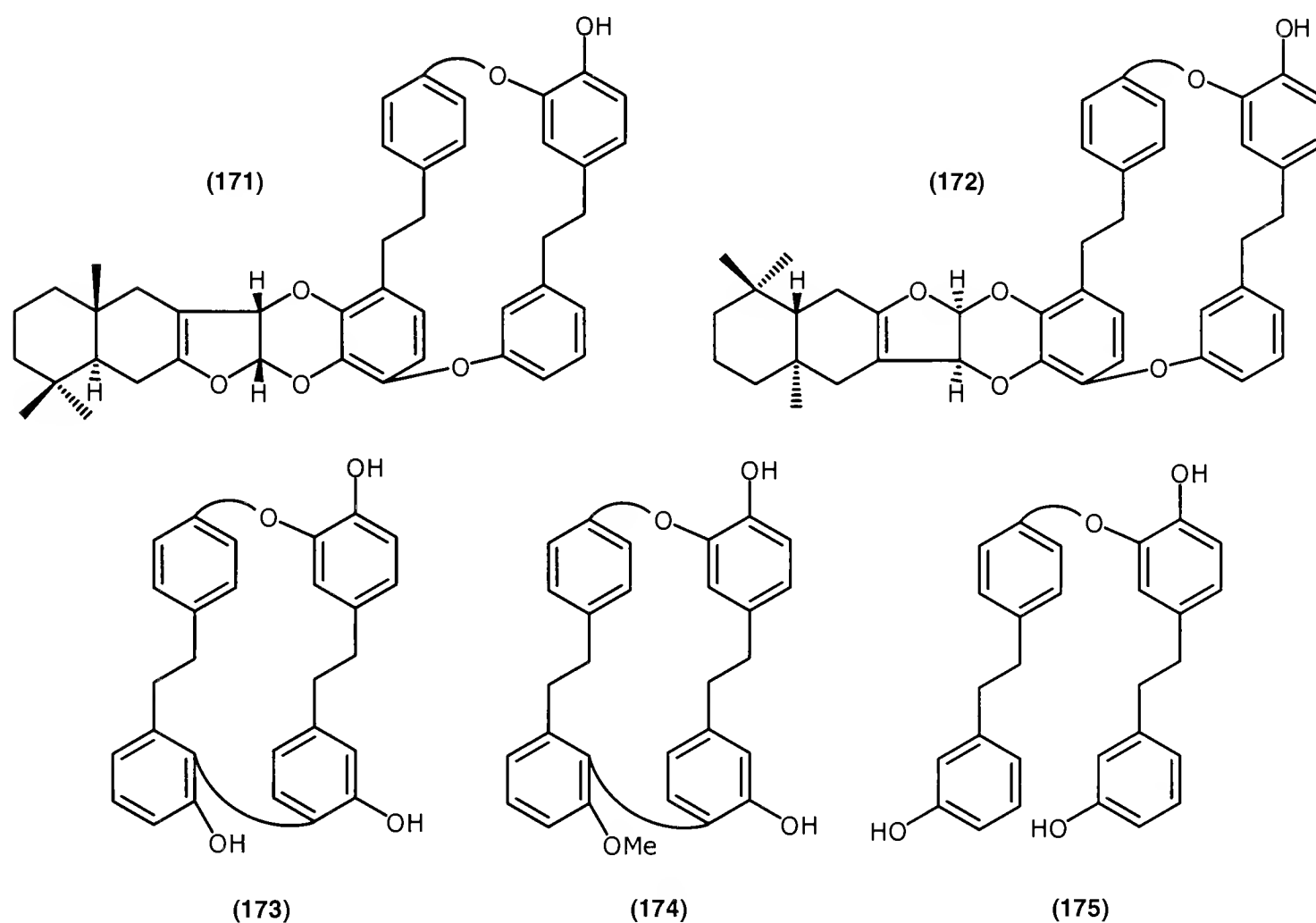
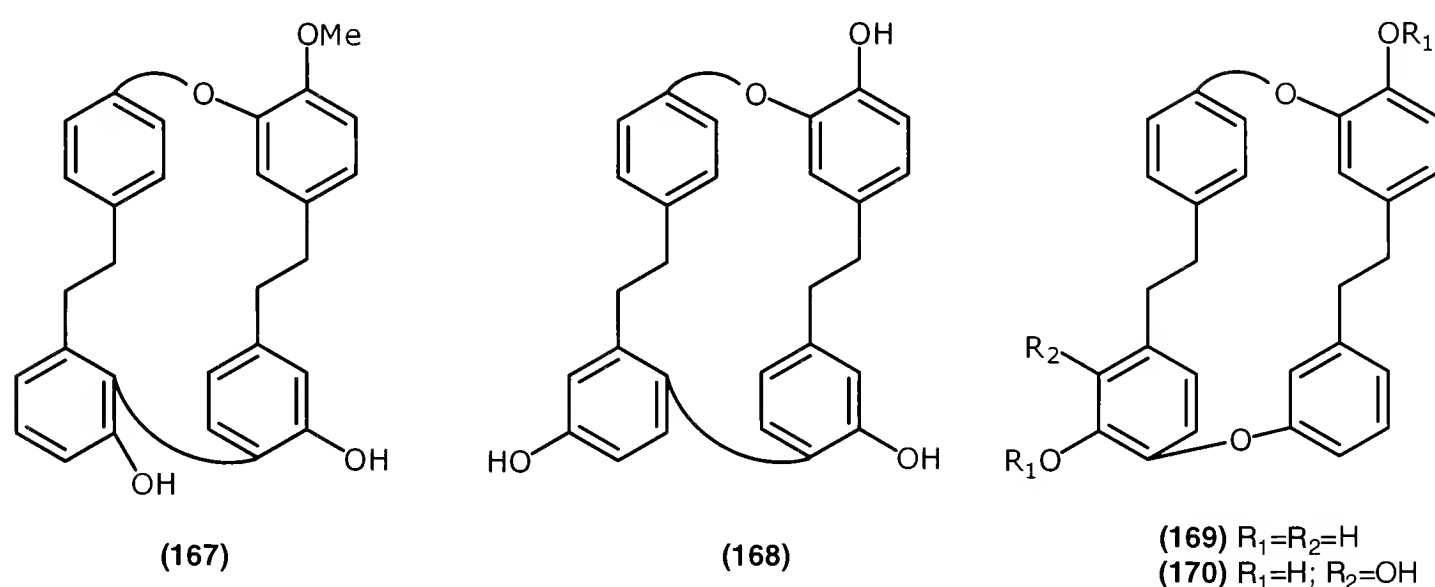
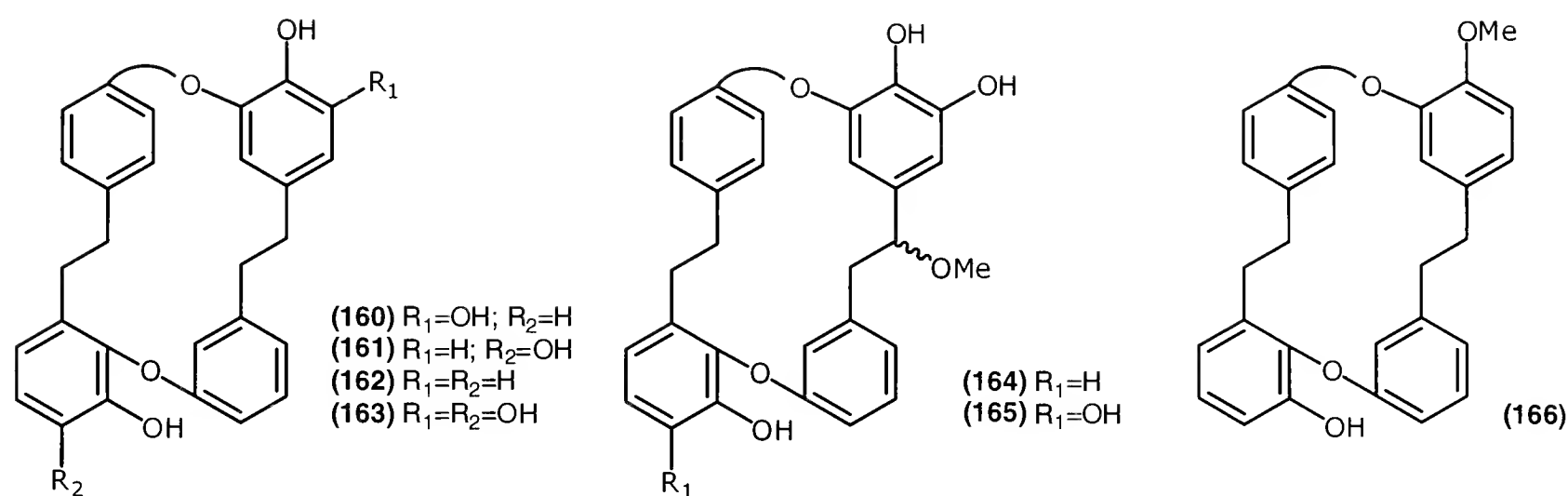
In several cases, aromatic compounds are valuable chemosystematic indicators, especially bibenzyl derivatives (Asakawa, 1995, 2004). *Radula* species are chemically quite distinct from the other liverworts because they elaborate the typical prenyl bibenzyl and related compounds (Asakawa, 1995, 2004). *Radula marginata* Taylor ex Gottsche, Lindenb. & Nees collected in New Zealand produces bibenzyl (148, 149) and bibenzyl cannabinoid, perrottetinene (147), which was first isolated from the Japanese *R. perrottetii* Gottsche ex Steph. (Asakawa, 1995, 2004), and its carboxylic acid (150) (Toyota et al., 2002). An unidentified New Zealand *Radula* species produces 3,5,4'-trihydroxy-4-(3,7,11-trimethyl-2,6,10-dodecatrienyl)bibenzyl (151) (Nagashima et al., 2006b). The species *R. appressa* Mitt. collected in Madagascar produces characteristic bibenzyl cannabinoids, *o*-cannabicyclol (152), and *o*-cannabichromene (153) (Harinantenaina et al., 2006b; Harinantenaina & Asakawa, 2007b).

Frullania species are rich sources not only of sesquiterpenoids and diterpenoids but also of



bibenzyl derivatives. Species in which the presence of bibenzyl derivatives was confirmed are placed in bibenzyl (type 3) or sesquiterpene lactone-bibenzyl chemotype (type 1) of *Frullania*. 3'4'-Methylenedioxy-3-methoxybibenzyl (**154**) was identified as a major component from the New Zealand *Frullania falciloba* (Asakawa et al., 1996), which was the same bibenzyl isolated from an Australian specimen (Asakawa et al., 1987a).

Compound **154** was detected as the major component in two other New Zealand *Frullania* species, *F. pycnantha* and *F. scandens* Mont. (Asakawa et al., 1996). The Australian *F. falciloba* produces two other bibenzyl derivatives, 3-hydroxy-4,3'-dimethoxybibenzyl (**155**) and 3-[4'-methoxybenzyl]-5,6-dimethoxyphthalide (**156**) (Asakawa et al., 1987a). From the Malaysian *F. serrata*, a new bibenzyl, 3,4,5,3',4'-pentamethoxybibenzyl (**157**),

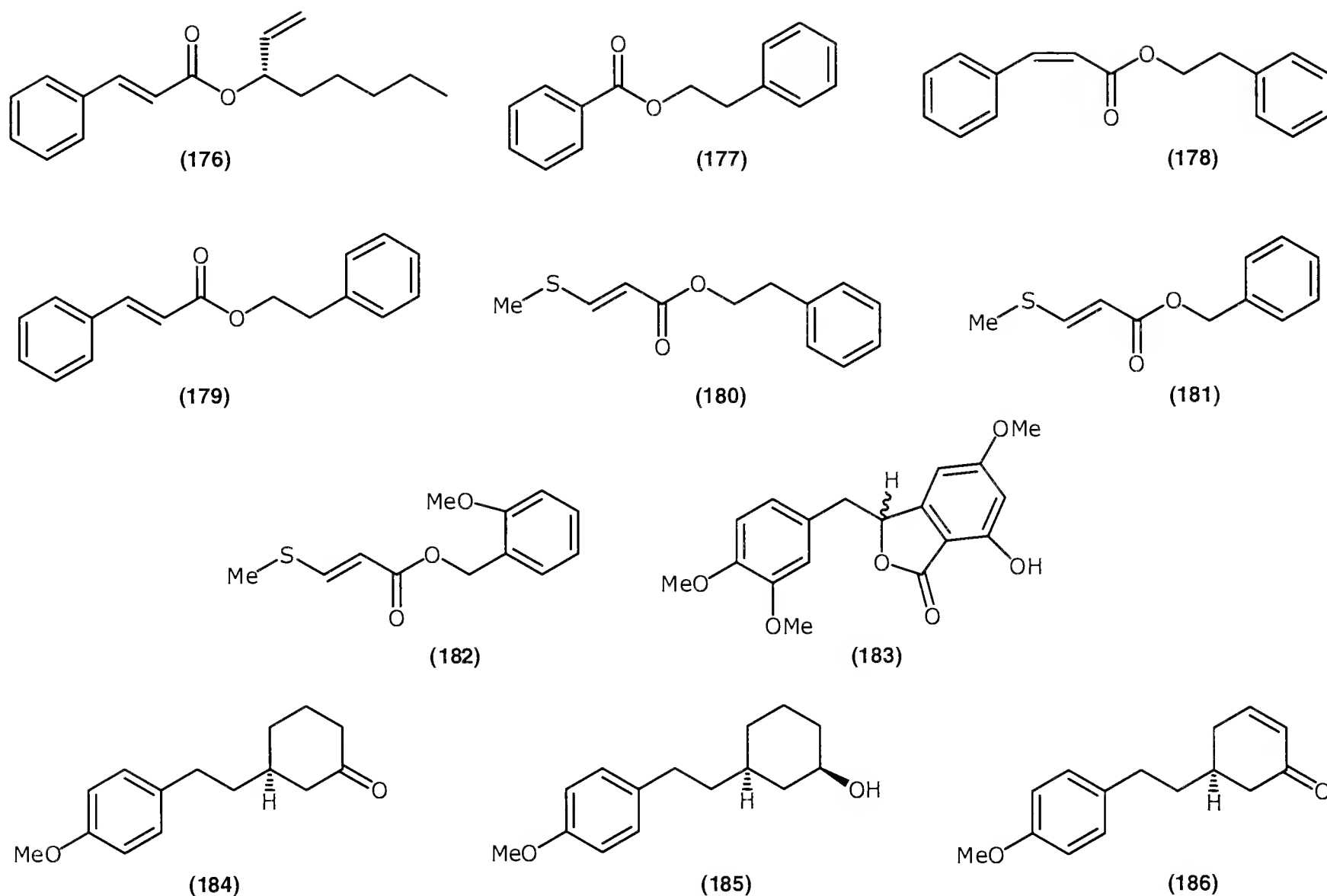


and brittonin B (**158**) have been isolated (Asakawa et al., 1991). Brittonin A and brittonin B (**158**) are the chemical markers of *F. brittoniae* A. Evans subsp. *truncatifolia* (Steph.) R.M. Schust & S. Hatt. (Asakawa et al., 1976).

The bibenzyl lunularin (**159**) has been detected in the New Zealand *Marchantia berteroana* Lehm.

& Lindenb.; however, 3-methoxy-4'-hydroxy-bibenzyl is a chemical marker of the New Zealand *Plagiochila stephensoniana* (Asakawa & Campbell, 1982).

The thalloid liverwort *Marchantia polymorpha* L. is widely distributed in the world and is a rich source of cyclic bis(bibenzyl)s (Asakawa, 1982a,

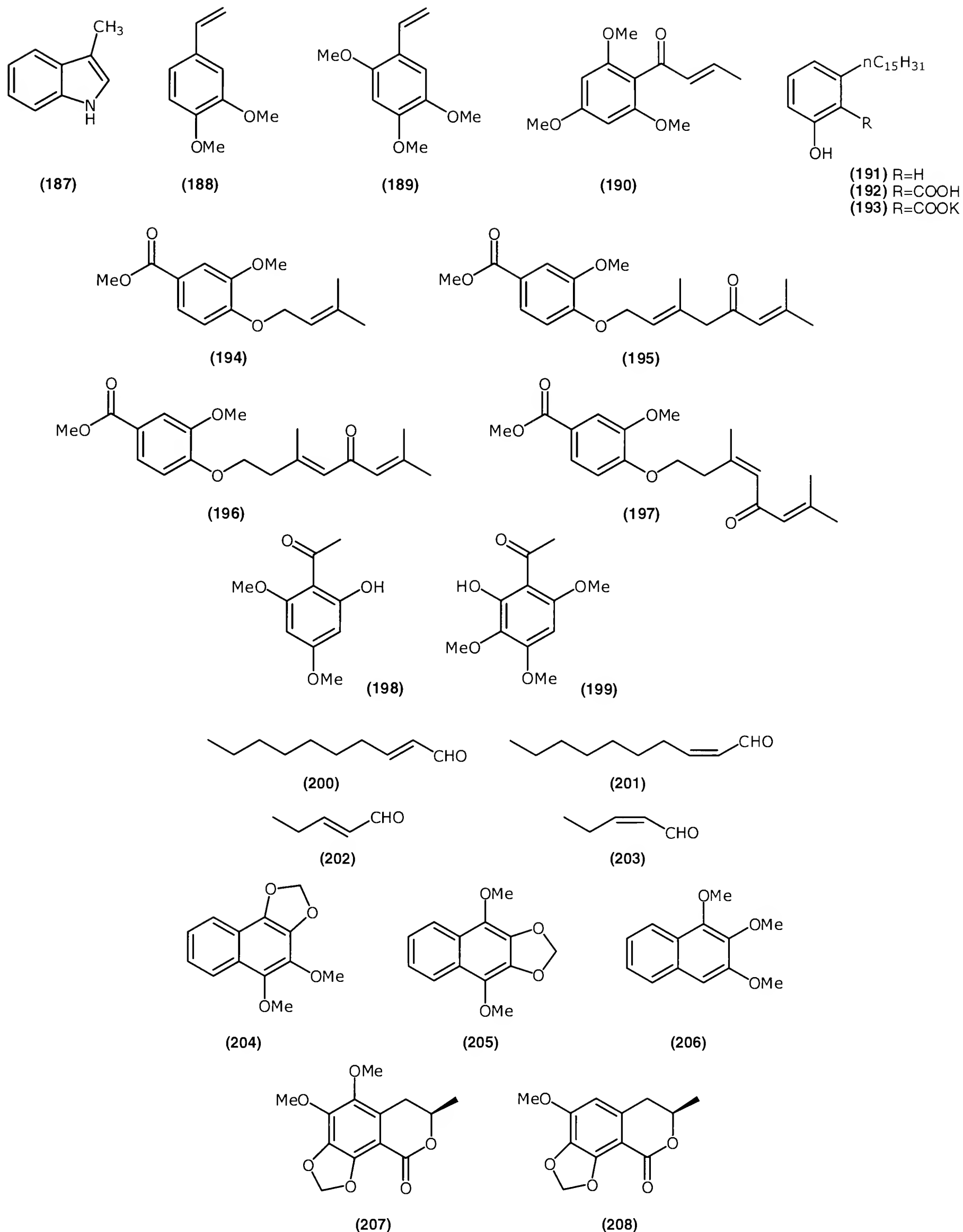


1995). The Japanese and German *M. polymorpha* produce marchantin A (**160**) as the major component. This compound has not been detected in South African species. Its place as the major cyclic bis(bibenzyl) is taken by marchantin H (**161**) (Asakawa et al., 1988a). Marchantin C (**162**) has been isolated from Indian *M. polymorpha*, marchantin E (**164**) from French species (Asakawa, 1995). It is obvious that the distribution of cyclic bis(bibenzyl)s of *M. polymorpha* is geographically differentiated, although the morphology of the species collected in the different countries are the same. The major component of Ecuadorian *Marchantia plicata* Nees & Mont. is marchantin A (**160**) (Nagashima et al., 1991a), while marchantin C (**162**) has been detected as the major component in the New Zealand *M. foliacea* Mitt. (Asakawa et al., 1996). Two new macrocyclic bis(bibenzyl)s, marchantin P (**166**) and riccardin G (**167**), have been isolated from *Marchantia chenopoda* collected in Venezuela (Tori et al., 1994a).

The Malaysian *Wiesnerella denudata* (Mitt.) Steph. elaborates not only germacranolides but also cyclic bis(bibenzyl)s, marchantins A (**160**) and B (**163**) (Asakawa et al., 1991). Marchantin B (**163**) along with marchantin K (**165**) and riccardin C (**168**) have been isolated from the Argentine *Plagiochasma rupestre* (Bardón et al., 1999b). The

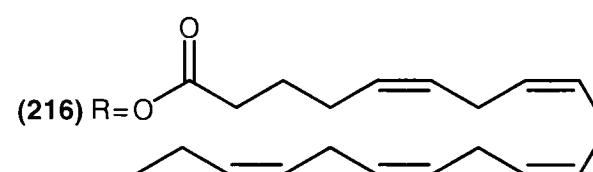
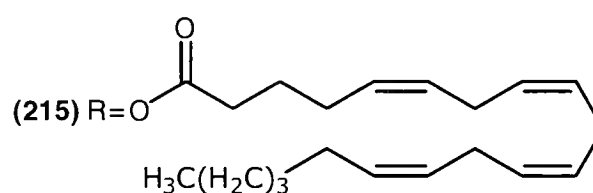
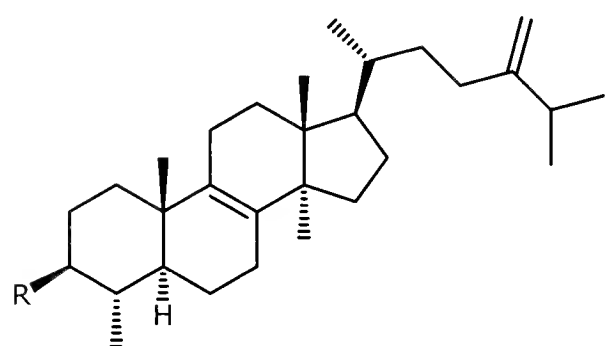
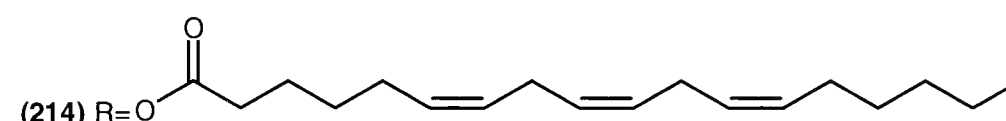
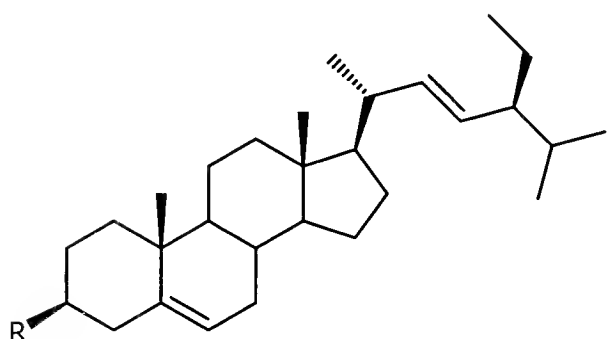
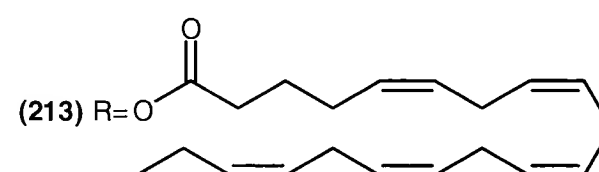
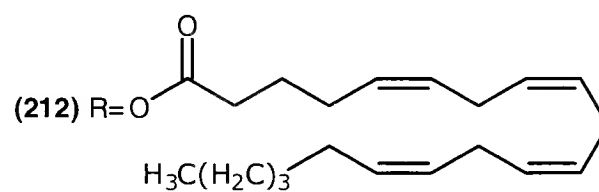
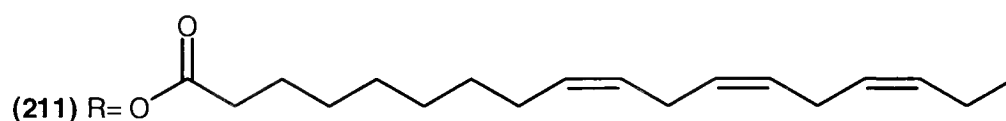
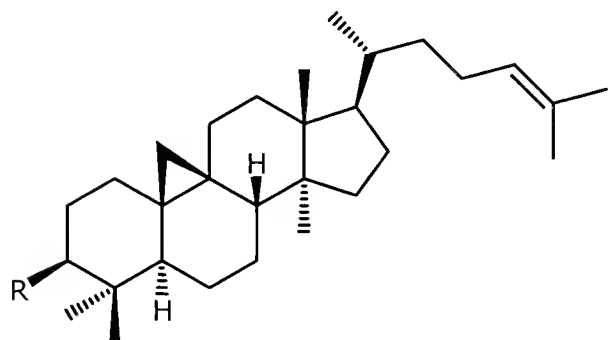
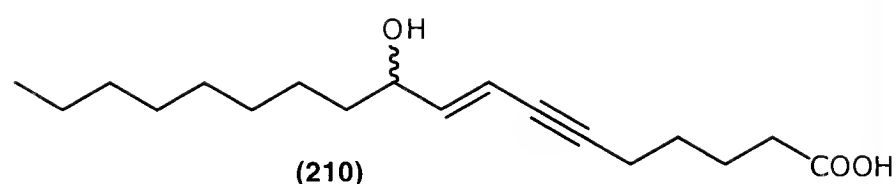
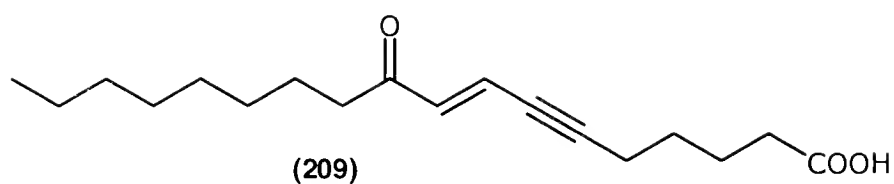
two Madagascar species *Plagiochila barteri* Mitt. and *P. terebrans* furnish marchantins C (**162**) and H (**161**) (Harinantenaina & Asakawa, 2007b). Neomarchantins A (**169**) and B (**170**) have been isolated from the New Zealand *Schistochila glaucescens* (Hook.) A. Evans (Asakawa, 1995). Further fractionation of the ether extract of this liverwort resulted in the isolation of sesquiterpene-bis(bibenzyl) compounds named glaucescens bis(bibenzyl) (GBB) A (**171**) and B (**172**) (Scher et al., 2002; Nagashima et al., 2004b). Two new cyclic bis(bibenzyl)s, riccardin D (**173**) and E (**174**), were isolated from the New Zealand large thalloid liverwort *Monoclea forsteri* Hook. together with the previously known riccardin C (**168**) and perrottetin E (**175**) (Toyota et al., 1988).

Besides bibenzyls and bis(bibenzyl)s, many other aromatic compounds are present in liverworts. The chemical markers of *Isotachis* are cinnamates and benzoates. The New Zealand *Isotachis lyallii* Mitt. in Hook. f. produces a new ester, 3(*R*)-1-octenyl cinnamate (**176**) (Asakawa et al., 2008). This compound has not been isolated from any other liverwort. The GC-MS of the ether extract of *I. aubertii* (Schwägr.) Mitt. collected from Madagascar showed the presence of β -phenethyl benzoate (**177**), β -phenethyl *cis*-cinnamate (**178**), and β -phenethyl *trans*-cinnamate



(179). This liverwort also biosynthesizes sulfur-containing acrylate, isotachin B (180) (Harianantenaina & Asakawa, 2004b, 2007b). Isotachin B (180) together with isotachin A (181) was previously isolated from the Japanese *Isotachis japonica* Steph. (Asakawa et al., 1985). This is the

first report of sulfur-containing compounds in bryophytes. The examination of the lipophilic components of a New Zealand liverwort *Balan-tiopsis rosea* Berggr. gave two new aromatic compounds, isotachin C (182) and balantiolide (183), together with isotachin A, isotachin B,



cinnamates, and benzoates (Asakawa et al., 1986). Three new *p*-substituted phenylethyl cyclohexane derivatives (**184–186**) have been isolated from this species by Nagashima et al. (2006b). *Balantiopsis rosea* is morphologically and also chemically very close to *Isotachis* species, with both genera classified in Balantiopsidaceae.

A small thalloid unidentified liverwort, an *Asterella*-like species collected in Malaysia, emits an intense unpleasant odor that is due to skatole (**187**) and represents 23% of the total extract. Occurrence of skatole in plants is very rare. This is the first identification of this compound in bryophytes. The major component (62%) of this liverwort was identified as 3,4-dimethoxystyrene

(**188**) (Asakawa et al., 1995). The presence of styrene derivatives as the major components has been detected in the Ecuadorian *Marchesinia brachiata* (Sw.) Schiffn. In addition to **188**, 2,4,5-trimethoxy-1-vinylbenzene (**189**) has been identified in this species (Nagashima et al., 1999). The other liverwort, *Hymenophyton flabellatum* (Labill.) Dumort. collected in New Zealand, produces the potent pungent phenyl butenone, 1-(2,4,6-trimethoxyphenyl)-but-2-en-1-one (**190**) (Asakawa et al., 2001).

Schistochila appendiculata (Hook.) Dumort. ex Trevis. is one of the chemically most distinct liverworts in the Jungermanniales because it produces long-chain alkyl phenols and their derivatives.

3-Undecyl phenol (**191**), 6-undecyl salicylic acid (**192**), and potassium 6-undecyl salicylate (**193**) have been isolated from this New Zealand liverwort (Asakawa et al., 1987b).

The most significant chemical markers of *Trichocolea* are prenyl ethers. Trichocolein (**194**) is the main component of the New Zealand *Trichocolea lanata*, while tomentellin (**195**) is the main component of *T. mollissima* (Asakawa et al., 1996). Reinvestigation of the New Zealand *T. mollissima* gave two other compounds, (*E*)-isotomentellin (**196**) and (*Z*)-isotomentellin (**197**) (Perry et al., 1996). Two hydroxyacetophenones, 2-hydroxy-4,6-dimethoxy acetophenone (**198**) and 2-hydroxy-3,4,6-trimethoxy acetophenone (**199**), have been isolated from the ether extract of the New Zealand *Plagiochila fasciculata* (Nagashima et al., 2004b).

Other Compounds

The New Zealand *Chiloscyphus pallidus* (Mitt.) J.J. Engel & R.M. Schust. emits very strong stink-bug smell when one crushes fresh material. The odor is due to the simple aliphatic aldehydes, (*E*)-dec-2-enal (**200**), (*Z*)-dec-2-enal (**201**), and (*E*)- (**202**) and (*Z*)-pent-2-enals (**203**), although the major component is (*E*)-dec-2-enal (**200**). These aliphatic aldehydes are characteristic chemical markers of this species (Asakawa et al., 1996). From the other New Zealand liverwort, *Wettsteinia schusteriana* Grolle, three naphthalene derivatives, wettsteins A–C (**204–206**) and two dihydroisocoumarin, 3(*R*)-methyl-5,6-dimethoxy-7,8-methylenedioxydihydroxyisocoumarin (**207**) and 3(*R*)-methyl-6-methoxy-7,8-methylenedioxy-dihydroxyisocoumarin (**208**), have been isolated (Asakawa et al., 1994a, 1994b). The naphthalene derivatives are very rare in bryophytes.

The New Zealand liverwort *Monoclea forsteri* does not biosynthesize any terpenoids. As mentioned before, it produces cyclic bis(bibenzyl)s and also fatty acids. Two new fatty acids, monocleic acid (**209**) with a conjugated yn-en-one chromophore and monocleolic acid (**210**) with yn-en-ol system, have been isolated from this liverwort (Toyota et al., 1988). Five new fatty acid esters of sterol or triterpenoid have been found in *Plagiochila circinalis* Lehm. & Lindenb. collected in New Zealand. They were shown to be cycloart-24-en-3 β -yl α -linolenate (**211**), cycloart-24-en-3 β -yl arachidonate (**212**), stignasteryl γ -linolenate

(**214**), 4 α ,14 α -dimethyl-8,24(28)-ergostadien-3 β -yl arachidonate (**215**), and 4 α ,14 α -dimethyl-8,24(28)-ergostadien-3 β -yleicosapentaenoate (**216**). Cycloart-24-en-3 β -yl eicosapentaenoate (**213**), which has been found in the Malagasy *Mastigophora diclados* (Harinantenaina & Asakawa, 2004a), was also isolated from *P. circinalis* (Toyota et al., 2006).

Discussion

The classification of the liverworts is often morphologically difficult since they have small gametophytes. Their terpenoids and aromatic metabolites, which constitute the oil bodies, are of value in taxonomic investigations. The liverworts occasionally produce their own peculiar constituents that have not been found in any other organisms. Sacculatane- and verrucosane-type diterpenoids and pinguisane- and myltaylane-type sesquiterpenoids have been found only in Marchantiophyta. Many of the compounds isolated from the liverworts have been represented by novel carbon skeletons, and many of these compounds are important chemical markers of each genus or family. *Isotachis* species produce aromatic esters, benzoates, and cinamates (**177–179**). The triterpene alcohol zeorin (**145**) is one of the chemical markers of genus *Plagiochasma*. The bibenzyls with a prenyl group (**148**, **149**, **151**) are the major components of *Radula* species, while prenyl ethers (**194–197**) are significant markers of *Trichocolea*. The major components of investigated *Frullania* species are sesquiterpene lactones (**33–43**) and bibenyls (**154–158**). Sesquiterpene caffeates (**88**, **89**) have been found only in *Bazzania* species, although chemical markers of this genus are bazzanane and cuparane sesquiterpenoids.

Many of the compounds isolated from southern hemispheric liverworts possess interesting biological activity (Asakawa, 2007). Mastigophorenes A (**25**), B (**26**), and D (**28**) from *Mastigophora diclados* exhibited neurotrophic properties at 10⁻⁵–10⁻⁷ M, greatly accelerating neuritic sprouting and network formation in the primary neuritic cell culture derived from the fetal rat hemisphere (Asakawa, 2007).

Finding new agents that inhibit NO production from natural sources is important in drug discovery; science overproduction of NO is involved in inflammatory disease. Sesquiterpene caffeates (**88**, **89**) present in *Bazzania* species have been shown to have anti-inflammatory effects by inhibition of prostaglandin E₂, nitric oxide, and

TNF- α production (Harinantenaina & Asakawa, 2007a). The strong inhibition of NO production in lipopolysaccharide (LPS)-stimulated RAW 264.7 cells was attributed to 2-geranyl-3,5-dihydroxybibenzyl (**149**) presence in Malagasy *Radula appressa* and New Zealand *R. marginata* (Harinantenaina et al., 2006b).

Frullania species are notable as liverworts that cause very intense allergic contact dermatitis. The allergy-inducing substances are sesquiterpene lactones. Such activity has also found in *Schistochila appendiculata*. The allergens of this species are long-chain alkylphenols (Asakawa, 1995, 2007). Strong growth-inhibitory activity of herbertenoids present in *Herbertus* species and also in *Mastigophora diclados* and *Dendromastigophora flagellifera* against pathogenic fungi is suggested to be due to the antioxidant properties of these compounds (Harinantenaina & Asakawa, 2007b).

Some *ent*-kaurane-type diterpenoids have been reported to possess antitumor activity (Asakawa, 2007). Jungermannones A-D (**112–115**) isolated from an unidentified *Jungermannia* species collected in New Zealand exhibited the cytotoxicity against HL-60 cells in a dose-dependent manner (Nagashima et al., 2005a).

Tomentellin (**195**) was the major cytotoxic component of *Trichocolea mollissima*, active against BSC cells at 15 mg/disk. Another prenyl ether, trichocolein (**194**), also showed the same activity (Perry et al., 1996). Marchantins A (**160**) and B (**163**) show DNA polymerase β inhibitory, cytotoxic, and anti-HIV-1 activity. Marchantin A (**160**) also shows muscle-relaxing activity (Asakawa, 2007). Riccardin C (**168**), distributed relatively widely in the Marchantiales and Metzgeriales, acts as a liver X receptor LXR α agonist and an LXR β antagonist, respectively, but efficiently enhances cholesterol efflux from THP-1 cell (Tamehiro et al., 2005).

Although liverworts are small plant groups, there are number of new terpenoids and aromatic compounds, several of which show interesting biological activity. At present, only 5% of the total bryophytes have been studied chemically.

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FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Three: Liverwort Chemistry and Physiology

Chapter Six: The Ascomycete *Rhizoscyphus ericae* Elicits a Range of Host Responses in the Rhizoids of Leafy Liverworts: An Experimental and Cytological Analysis

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Abstract

Ascomycete fungi, identified cytologically from their simple septa and Woronin bodies and genetically diagnosed as belonging to the *Rhizoscyphus ericae* (D. J. Read) W. Y. Zhuang & Korf (*Hymenoscyphus ericae* (D. J. Read) Korf & Kernan) aggregate form a range of specialized mutualistic associations with the rhizoids in several families of leafy liverworts. To test the hypothesis that this fungus can produce these associations between liverworts from widely separate geographical regions, we carried out cross-infection experiments between mycobionts that induce branching and septation in the rhizoids in the Schistochilaceae from the southern hemisphere and those from a range of disparate taxa (*Bazzania*, *Calypogeia*, *Cephalozia*, *Kurzia*, *Lepidozia*, *Odontoschisma*) from the northern hemisphere and from *Calluna* in the Ericaceae. All the fungal isolates produced rhizoid infections identical to those found in nature. The same fungal isolates also invaded the rhizoids of axenically cultured *Nardia scalaris*, whose stems in nature harbor a basidiomycete and the fungus-free species *Jungermannia gracillima*, but

balanced relationships in these cross infection experiments were not established. Consideration of recent liverwort phylogenies placing the Schistochilaceae as sister to all the other fungus-containing clades of leafy liverworts, together with dating of this family in the Triassic, suggests that liverwort–ascomycete associations may have pre-dated ericoid mycorrhizas. However, the diverse cytology of these associations and their discontinuous distribution between families in the leafy liverworts indicate more recent and multiple origins including host swapping from the Ericales.

Introduction

Liverworts form a remarkable range of permanent relationships with fungi. Glomeromycetes occur within the thalli of the majority of the Marchantiophyta (Ligrone et al., 2007), whereas basidiomycetes are found in the stems of a few families in the Jungermanniidae (Kottke et al., 2003; Nebel et al., 2004; Kottke & Nebel 2005; Duckett et al., 2006a) and in the thalli of the Aneuraceae (Ligrone et al., 1993; Read et al., 2000). All three of these associations have many cytological features in common with their mycorrhizal counterparts in vascular plants. The majority of the basidiomycete associations investigated to date seem to be host specific (Duckett et al., 2006a), with the striking exception of the *Cryptothallus* fungus which also forms typical ectomycorrhizas with *Betula* (Bidartondo et al., 2003). In contrast, the same *Glomus* species appears to occur in liverworts, pteridophytes, gymnosperms, and angiosperms (Russell & Bulman, 2005).

Ascomycetes, identified by the presence of simple septa and Woronin bodies from electron microscope studies (Duckett et al., 1991), are found in several families of leafy liverworts. Cross-infection experiment studies have demonstrated that the rhizoidal ascomycetes have a wide host range extending to the Ericales (Duckett & Read, 1995). This has subsequently been confirmed by sequencing studies revealing that these all belong within the *Rhizoscyphus ericae* (D. J. Read) W. Y. Zhuang & Korf (*Hymenoscyphus ericae* [D. J. Read] Korf & Kernan) aggregate (Kottke & Nebel, 2005; Upson et al., 2007; Pressel et al., 2008; Bidartondo & Duckett, unpublished data). In terms of their location, the ascomycete infections in leafy liverworts are without parallel elsewhere in land plants. They are strictly confined to the rhizoids where the presence of the fungus induces various deformations including swelling and branching (Pocock & Duckett, 1985). In *Lepidozia* and *Kurzia*, however, swollen rhizoids are produced in the absence of the

fungus. At the rhizoid bases in some genera, such as *Calypogeia* and *Odontoschisma*, spread of the hyphae beyond the rhizoids is prevented by prominent overgrowths of host wall material (Němec, 1899, 1904) like those produced by mosses and liverworts as defense mechanisms against pathogenic fungi (Martinez-Abigair et al., 2005). Most remarkable of all the ascomycete associations are those in the Schistochilaceae, where the fungus induces both branching and septation at the tips of the rhizoids (Pressel et al., 2008). Outside the Schistochilaceae, septate rhizoids are known only in *Arachniopsis*, *Acromastigum* (Lepidoziaceae) (Schuster 1965; Kitagawa & Kodama, 1974), *Xenochila* (Plagiochilaceae) (Degenkolbe, 1938), and *Vetaforma* (Lepicoleaceae) (Fulford & Taylor, 1960).

Ultrastructural studies have revealed significant cytological differences in fungal association morphology between taxa. In *Cladopodiella fluitans*, the fungus forms a pseudoparenchymatous sheath in copious mucilage around the bulbous tips of the rhizoids with very few hyphae penetrating the walls (Duckett et al., 1991), whereas in *Cephalozia connivens*, the rhizoids lack the investiture of mucilage, and their swollen tips are packed with hyphae (Read et al., 2000). In both *Cladopodiella* and *Odontoschisma*, the host cytoplasm in the cells at the base of the rhizoids contains numerous mitochondria adjacent to the pegs of host wall that prevent the further ingress of the fungal hyphae (Duckett et al., 1991). In infected rhizoids of *Pachyschistochila*, a prominent interfacial matrix develops around the hyphae, and this is the only example known to date among the fungal associations in leafy liverworts where the host breaks down and digests aging hyphae (Pressel et al., 2008). This phenomenon, in contrast, is the rule in the glomeromycete infections in thalloid taxa (Read et al., 2000; Carafa et al., 2003; Duckett et al., 2006b; Ligrone et al., 2007).

Although there are extensive cytological, experimental, and molecular data on ascomycete-containing liverworts from the northern hemisphere (Kottke & Nebel, 2005) similar information

for the south is limited to the identification of *Rhizoscyphus* from *Cephaloziella varians* from Antarctica (Chambers et al., 1999; Upson et al., 2007) and two Chilean *Pachyschistochila* species (Pressel et al., 2008). Reciprocal cross-infection experiments on the latter produce identical branching and septation of the rhizoids. However, we do not know whether the *Pachyschistochila* fungus is able to produce typical ericoid mycorrhizas and typical rhizoid infections in other liverworts, particularly northern hemisphere taxa, and vice versa. *Rhizoscyphus ericae* is an aggregate of closely related taxa only some of which form ericoid mycorrhizas (Vralstad et al., 2001). It is therefore of interest to find out whether the northern hemisphere fungus is able to form associations with southern hemisphere liverworts that contain rhizoidal ascomycetes.

The aims of the work described here were 1) to explore the extent of host sharing across liverworts from both hemispheres and the Ericales via cross-infection experiments on a range of axenically cultured northern hemisphere genera, *Pachyschistochila*, and roots of a representative member of the Ericales (*Calluna vulgaris*); 2) to collect ultrastructural data on hitherto unstudied ascomycete–rhizoid associations; 3) to explore whether the resulting comparative information points to single or multiple evolution of liverwort–ascomycete associations; and 4) to compare the cytology of the natural ascomycete rhizoid associations with those produced artificially in culture between a liverwort that in nature contains a basidiomycetous endophyte (*Nardia scalaris*) and one that is fungus-free (*Jungermannia gracillima*). In a previous study (Duckett et al., 2006a), these were the only taxa in these categories that developed swollen rhizoids when infected with ascomycetes.

Materials and Methods

Authorities for liverwort specific names are given here. Authorities for liverwort genera mentioned elsewhere in the text follow Crandall-Stotler and Stotler (2000). For the cross-infection experiments, plants of *Pachyschistochila subimmersa* Schuster and Engel and *P. splachnophylla* Schuster and Engel were collected from Tierra del Fuego, Chile. Those of *Bazzania trilobata* (L.) Gray, *Calypogeia fissa* (L.) Raddi, *Cephalozia bicuspidata* (L.) Dumort., *C. connivens* (Dicks.)

Lindb., *Jungermannia gracillima* Sm., *Kurzia pauciflora* (Dicks.) Grolle, *Lepidozia reptans* (L.) Dumort., *Lophozia ventricosa* (Dicks.) Dumort., *Nardia scalaris* Gray, *Odontoschisma denudatum* (Mart.) Dumort., and *Calluna vulgaris* L. were collected from sites in Britain. Specimens of all materials used in this study are in the herbarium of J. G. Duckett. Rhizoids from wild-collected *Pachyschistochila succulenta* Engel and Schuster (from the Arthur's Pass region, South Island, New Zealand) and various resynthesized associations (Table 1) were fixed and embedded for transmission electron microscopy (TEM) as described previously (Carafa et al., 2003). Scanning electron microscopy was carried out on critical point dried axenic and reinfected rhizoids of *Pachyschistochila subimmersa* and *P. splachnophylla*.

To examine the effects of fungi on their hosts, the liverworts (Table 1) were first grown axenically on 1/10 Parker nutrient medium solidified with 1% Phytagel (Sigma). The axenic cultures of *Calypogeia fissa* and *Odontoschisma denudatum* were obtained from gemmae surface sterilized in 1.5% sodium hypochlorite solution for 30 seconds. After 2 weeks germinating, gemmae with neither fungal nor bacterial contaminants were subcultured onto new Phytagel plates. Cultures of all the remaining taxa were initiated from spores following surface sterilization of undehisced capsules in 1.5% sodium hypochlorite solution for 2 minutes (for further detailed methodology, see also Duckett et al., 2006a). The cultures were maintained at 15°C with constant illumination beneath fluorescent lighting with an irradiance of 50 W m⁻².

Liverwort ascomycetes were isolated by surface sterilizing individual rhizoids in 1.5% hypochlorite for 2–3 minutes. Following thorough washing in sterile distilled water, the rhizoids were planted onto 1% Phytagel containing no nutrients (Duckett & Read, 1995). The basidiomycete endophyte in *Lophozia ventricosa* was isolated as described previously (Duckett et al., 2006a). Sequencing (Bidartondo & Duckett, unpublished data) confirmed that the rhizoidal fungi *in situ* and in the cultures belonged to the *Rhizoscyphus ericae* agg., while those from *Lophozia ventricosa* were members of the Sebacinaceae as reported previously (Kottke et al., 2003).

In the resynthesis experiments fungal isolates (four from each liverwort) were added to 3-month-old liverwort cultures (four for each fungus) between 5 and 10 mm in diameter. The

TABLE 1. Resynthesis of hepatic-fungus associations *in vitro* using host and nonhost fungi. N/A = not applicable; \pm a = occasional swollen rhizoids.

Family	Species	Natural association	Own associate	Pachyschisto- <i>chila</i>			Ascomycete isolates from			Morphological response of host rhizoids to fungal infections
				<i>subimmersa</i> isolate	<i>splachnophylla</i> isolate	<i>chila</i> isolate	<i>Kurzia</i> , <i>Lepidozia</i> , <i>Cephalozia</i> , and <i>Calypogeia</i> , and <i>Odontoschisma</i>	<i>Rhizoscyphus</i> from <i>Calluna vulgaris</i>	<i>Lophozia ventricosa</i> isolate	
Schistochilaceae	<i>Pachyschistochila subimmersa</i>	Ascomycete	+	+	+	+	+	+	-	Branching and septation
	<i>P. splachnophylla</i>	Ascomycete	+	+	+	+	+	+	-	Branching and septation
	<i>Lepidozia reptans</i>	Ascomycete	+	+	+	+	+	+	-	Swollen tips
Lepidoziaceae	<i>Kurzia pauciflora</i>	Ascomycete	+	+	+	+	+	+	-	Swollen tips
	<i>Bazzania trilobata</i>	Ascomycete?	+	+	+	+	-	+	-	No morpho-logical change
	<i>Calypogeia fissa</i>	Ascomycete	+	+	+	+	+	+	-	Slightly swollen tips
Cephaloziaceae	<i>Cephalozia bicuspidata</i>	Ascomycete	+	+	+	+	+	+	-	Irregularly swollen tips
	<i>C. connivens</i>	Ascomycete	+	+	+	+	+	+	-	Irregularly swollen tips
	<i>Odontoschisma denudatum</i>	Ascomycete	+	+	+	+	+	+	-	No morpho-logical change
Jungermanniaceae	<i>Jungermannia gracillima</i>	None	N/A	\pm a	\pm a	\pm a	\pm a	\pm a	-	Slightly swollen tips
	<i>Nardia scalaris</i>	Basidiomycete	+	\pm a	\pm a	\pm a	\pm a	\pm a	-	Slightly swollen tips
	<i>Lophozia ventricosa</i>	Basidiomycete	+	-	-	-	-	-	+	No morpho-logical change
Ericaceae	<i>Calluna vulgaris</i>	Ascomycete	+	+	+	+	+	+	-	N/A

ability to reproduce rhizoidal associations like those found in nature was monitored over a 6-month period. All the replicates gave identical results. Selected resyntheses were fixed and embedded for TEM and their cytology compared to wild specimens.

Results

The results of the reinfection experiments and the effects of fungus on rhizoid morphology are summarized in Table 1. The rhizoidal ascomycetes produced typical infections (for details, see Duckett & Read, 1995) when introduced into axenic cultures of both their original host liverwort and all the other liverworts that normally contain rhizoidal fungi. *Rhizoscyphus* from *Calluna* also infected all the same liverworts. In contrast, the basidiomycete from *Lophozia ventricosa* failed to penetrate the rhizoids of any of these liverworts, and conversely none of the ascomycetes entered the *Lophozia* rhizoids. The ascomycete isolates did, however, infect the rhizoids of the normally fungus-free *Jungermannia gracilima* and *Nardia scalaris* (Fig. 1N), whose stems contain a basidiomycete. Further examples of successful reinfections between liverworts and ascomycetes can be found in Duckett and Read (1995).

Representative examples of the morphology of axenically cultured rhizoids, their wild counterparts, and those reinfected with fungus in culture are illustrated in Figure 1. In most species, uninfected rhizoids are nonswollen and unbranched (Fig. 1A, G) with an ovoid nucleus lying along the lateral wall next to a large central vacuole. Exceptions are *Kurzia*, *Lepidozia*, and *Cladopodiella fluitans*, which produce swollen rhizoids even in the absence of the fungus, and in the latter species these are heavily invested in mucilage (Duckett et al., 1991). The presence of the fungus from both *Pachyschistochila* species (Fig. 1C, D), those from other liverworts (Fig. 1D, E), and the endophyte from *Calluna* (Fig. 1F) induces septation and branching exactly like what is found in nature (Figs. 1B, 2A–C). In *Cephalozia* (Figs. 1H, I, 2D) and *Calypogeia* (Duckett et al., 1991), swelling and deformation of rhizoid apices occurs only after these have become heavily infected, while infected rhizoids remain largely unaltered in *Odontoschisma* (Fig. 1M) and *Bazzania*. In the last genus, reinfected rhizoid tips remain

unbranched unless they grow into contact with the walls of the culture vessel, mirroring the situation in nature where branching occurs only when the rhizoids produced in fascicles on flagelliform branches grow onto other bryophytes (Pocock & Duckett, 1985) (Fig. 2E, F). The present experiments demonstrating that living *Bazzania* rhizoids are regularly reinfected indicate that this genus almost certainly forms natural associations with an ascomycete. Previous studies suggested that in *Bazzania*, fungal colonization might only occur in dead rhizoids (Duckett et al., 1991).

The presence of simple septa with Woronin bodies in all the wild-collected liverworts and in all the reinfection experiments (Fig. 3A) confirms all the fungi as ascomycetes. The septate rhizoid tips of *Pachyschistochila* (Fig. 3B, C) are packed with healthy hyphae 1–2 μm in diameter surrounded by electron-dense host cytoplasm. Older hyphae are surrounded by a prominent interfacial matrix with a highly irregular outline (Fig. 3C). Subsequently, the hyphae degenerate, while the host cytoplasm remains alive (Pressel et al., 2008). There is no evidence of multiple infection cycles in *Pachyschistochila* or any of the other liverworts with rhizoidal ascomycetes.

The swollen-tipped wild and artificially reinfected rhizoids of *Cephalozia connivens* (Fig. 3D) and *C. bicuspidata* (not illustrated) are thin walled and packed with healthy hyphae 1–2 μm in diameter. Adjacent to fungal penetration sites, the host wall forms an electron-dense investiture around the invading hyphae (Fig. 3E, F), whereas deeper within the rhizoids, the hyphae are surrounded by a less dense interfacial matrix 100–150 nm thick. The host cytoplasm adjacent to the hyphae contains a highly pleomorphic centrally placed nucleus with dispersed chromatin (Fig. 3I), elongate mitochondria with prominent saccate cristae, and ovoid plastids 1–1.5 μm in diameter with small grana. Further conspicuous features of the host cytoplasm are dictyosomes with large vesicles, presumably contributing to the interfacial matrix (Fig. 3G), and partially coated reticulum (Fig. 3H).

The less swollen infected rhizoid tips in *Calypogeia* are similarly packed with hyphae (Fig. 4A). The host cytoplasm is similar to that in *Cephalozia* except that the plastids are packed with starch grains (Fig. 4B). At fungal entry points, the hyphae are constricted down to a diameter of less than 0.5 μm and are surrounded by extremely dense host wall material (Fig. 4C). This figure also shows that, similar to *Cladopodiella*

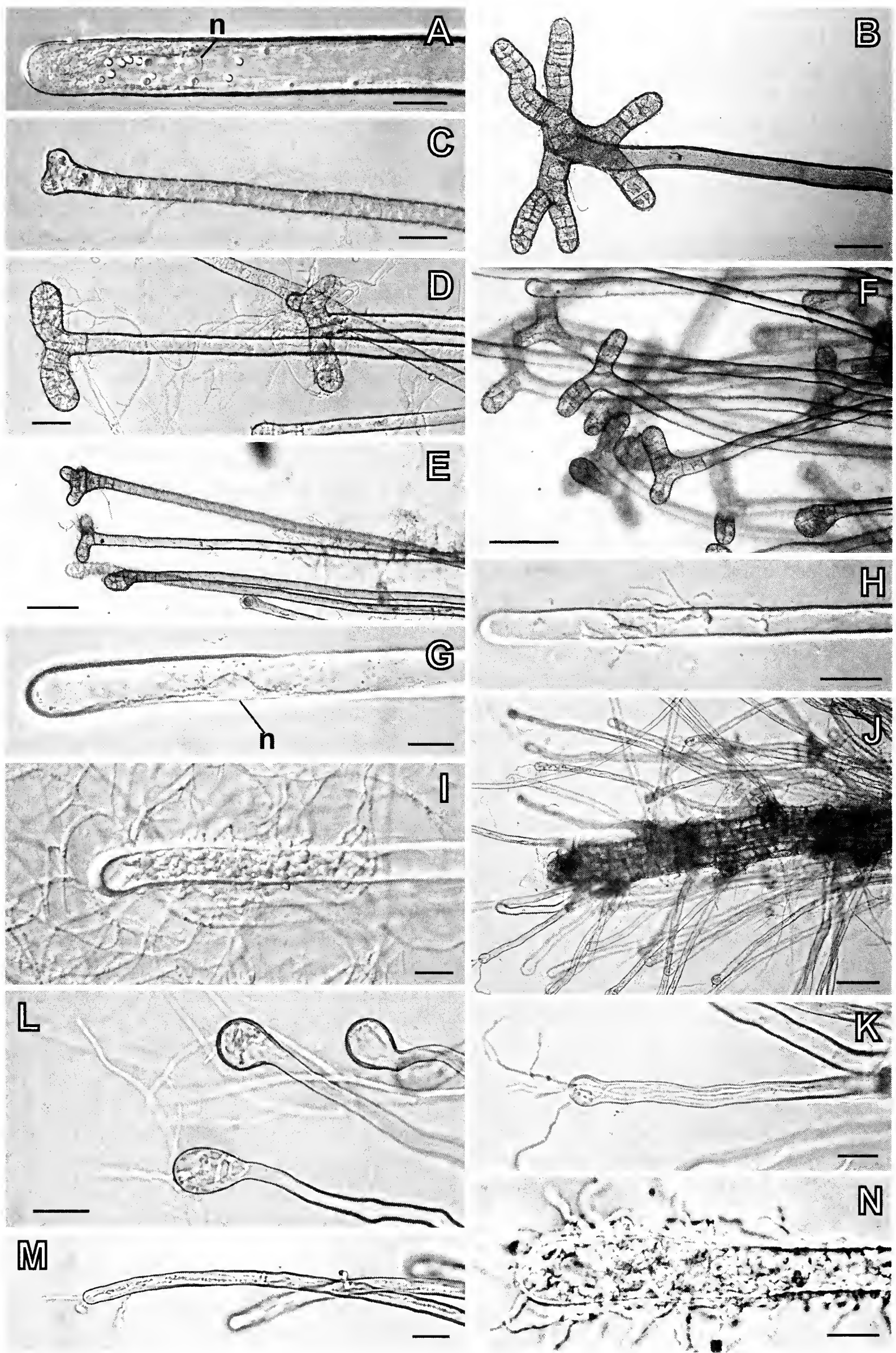


FIG. 1. Light micrographs illustrating the morphology of various rhizoid apices. (A, B) *Pachyschistochila splachnophylla*. (A) Unbranched nonseptate rhizoid from an axenic culture; n, nucleus. (B) Branched and septate wild rhizoid. (C) *Pachyschistochila subimmersa*, onset of rhizoid branching in the presence of the fungus from *Cephalozia bicuspidata*. (D–F). *Pachyschistochila splachnophylla*, branched and septate rhizoids produced in culture in the presence of fungi from *Odontoschisma denudatum* (D), *Lepidozia reptans* (E), and *Calluna vulgaris* (F). (G–I) *Cephalozia bicuspidata*. (G) Uninfected rhizoid from an axenic culture. n, nucleus. (H, I) Early and later stages in reinfection

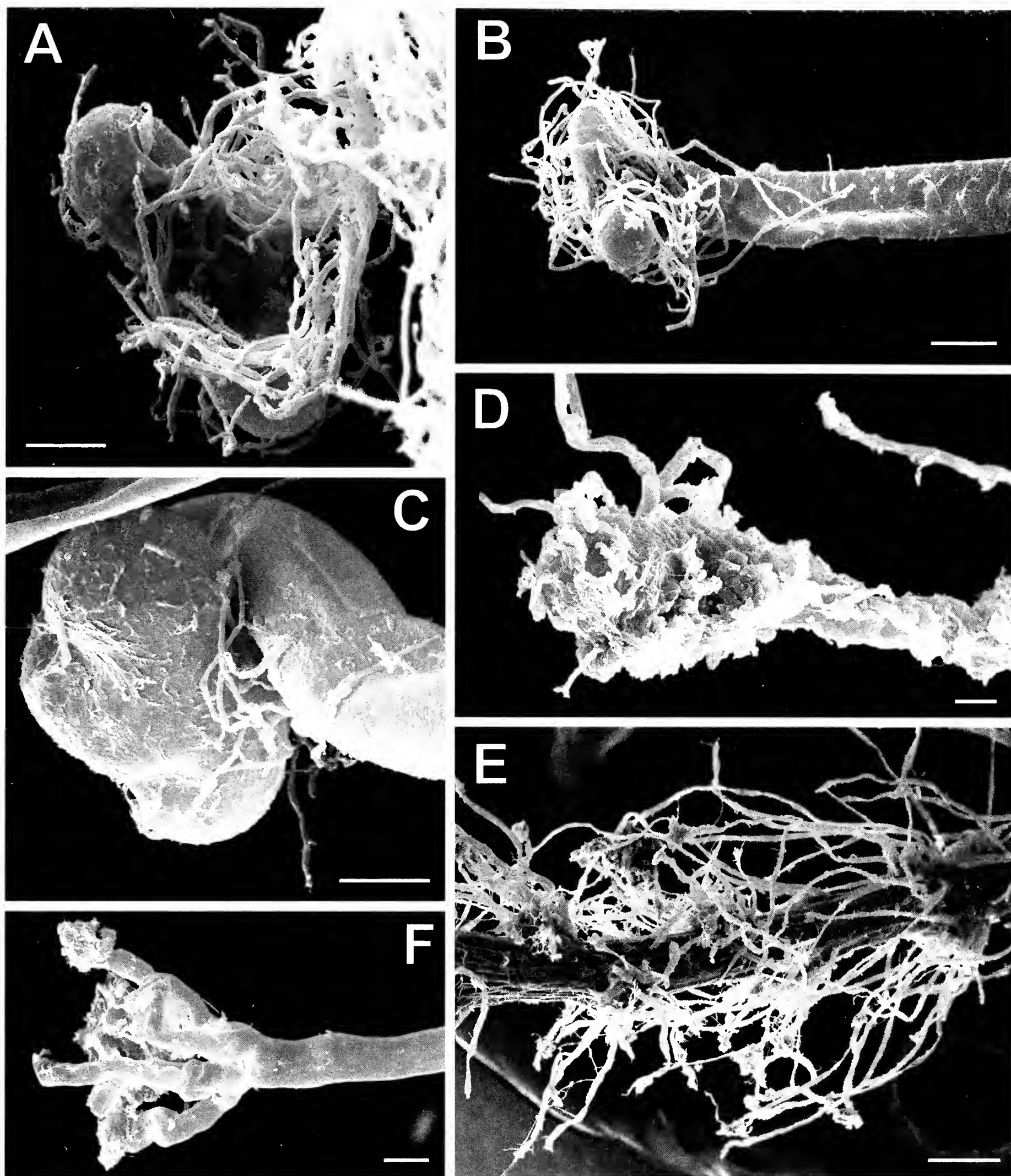


FIG. 2. Scanning electron micrographs of fungus infected rhizoid apices. (A, B) *Pachyschistochila subimmersa*. (A) Axenically cultured rhizoid reinfected with its own fungus. (B) Wild-collected rhizoid. (C) *Pachyschistochila splachnophylla*, axenically cultured rhizoid reinfected with its own fungus. (D) *Cephalozia bicuspidata*, wild rhizoid. (E, F) *Bazzania trilobata*. (E) Flagelliform axis with fascicles of branched rhizoids. (F) Wild branched rhizoid tip. Scale bars: E = 200 μ m; A–D, F = 20 μ m.

with the fungus from *Pachyschistochila splachnophylla*. (J, K) *Lepidozia reptans*. (J) Flagelliform axis with numerous rhizoids infected with the fungus from *Pachyschistochila splachnophylla*. (K) Detail of an infected rhizoid. (L) *Kurzia pauciflora* infected with the fungus from *Pachyschistochila splachnophylla*. (M) *Odontoschisma denudatum* with the fungus from *Pachyschistochila splachnophylla*. (N) *Nardia scalaris* infected with *Rhizoscyphus* from *Calluna*. Scale bars: E, F = 100 μ m; A, G, I, K, L, N = 20 μ m; B, D, H, J, M = 50 μ m.

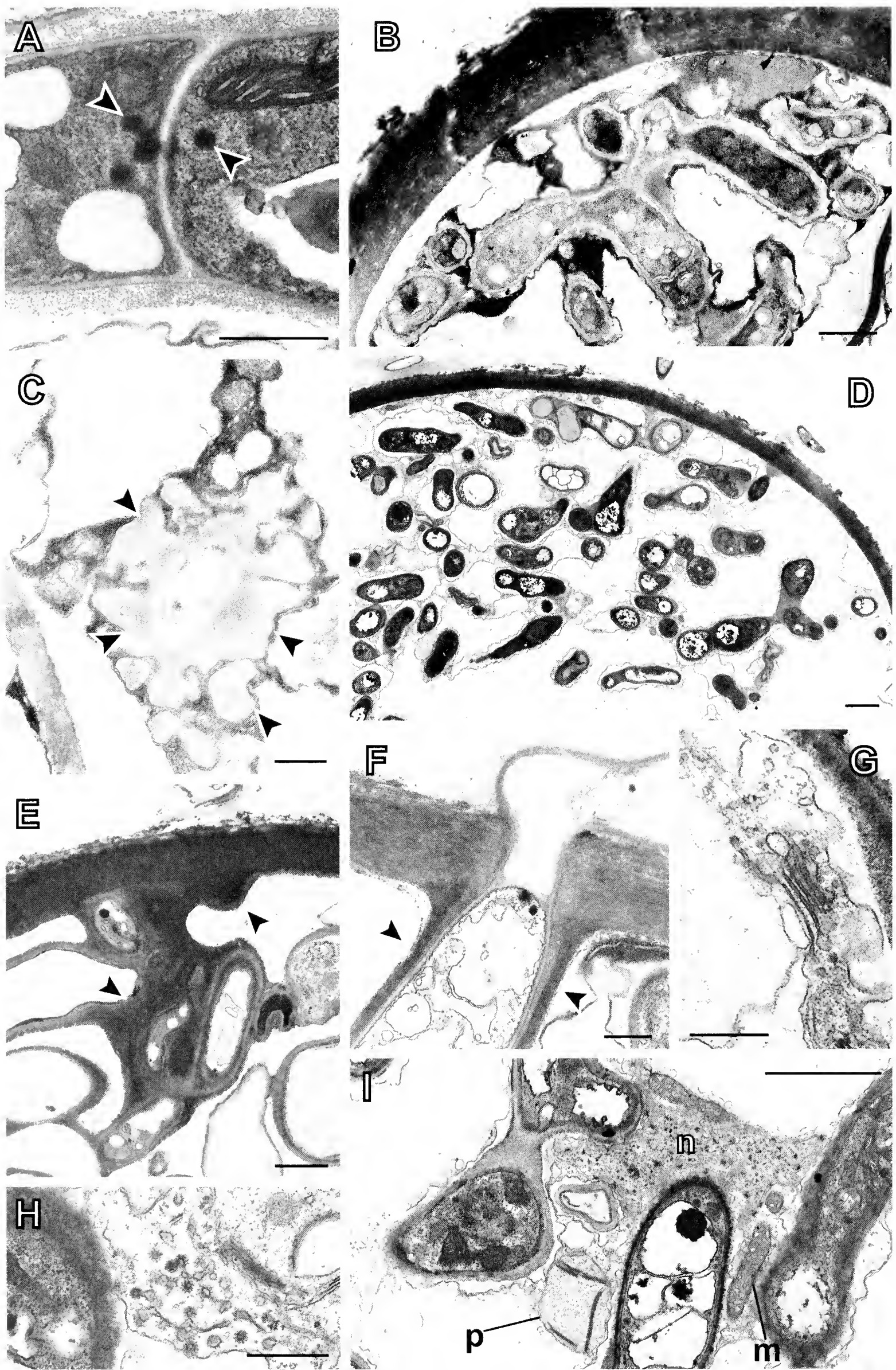


FIG. 3. Transmission electron micrographs of ascomycete-infected rhizoids. (A) Typical simple septum with Woronin bodies (arrowed); *Cephalozia connivens* reinfected with *Rhizoscyphus*. (B, C) *Pachyschistochila splachnophylla*. (B) Numerous hyphae in a rhizoid apex. (C) Labyrinthine interfacial matrix (arrowed) around a hypha. (D–I) *Cephalozia connivens*. (D) General aspect of wild swollen rhizoid apex packed with hyphae. (E–I) Rhizoids reinfected with *Rhizoscyphus* from *Calluna*. (E) Massive overgrowths of host wall material (arrowed) near a hyphal penetration site. (F) Collar of host wall material (arrowed) around a penetrating hypha. (G, H) Dictyosome and partially coated reticulum in the cytoplasm of infected rhizoids. (I) Pleomorphic nucleus (n) and a plastid (p) with small grana adjacent to infecting hyphae; m = mitochondrion. Scale bars: B, D, E, I = 2 μ m; A, C, F–H = 0.5 μ m.

fluitans (Read et al., 2000), the outer wall of the rhizoid apex is highly mucilaginous. At the base of the rhizoids, penetration of hyphae into the stem cells is prevented by overgrowths of wall material (Fig. 4D) exactly like those recorded by Němec (1899, 1905). The only difference between the infected rhizoids of *Odontoschisma* (Fig. 4E) and *Cephalozia* is that the plastids adjacent to the hyphae in the former genus are plate-like and up to 5 µm in diameter. Overgrowths of fibrillar host wall material are associated with hyphal penetration sites in ericaceous hair roots (Fig. 4F).

The cytology of noncompatible rhizoid infections is rather different (Fig. 5). Within the infected rhizoid tips in *Jungermannia gracillima* (Fig. 5A), there is very little hyphal proliferation, and around their periphery are numerous sites where fungal entry has been prevented by host wall overgrowths (Fig. 5B). Swollen rhizoids of *Nardia scalaris* infected with the ascomycetes from other liverworts contain similar numbers of hyphae to those seen in *Cephalozia* and *Odontoschisma* (Figs. 3D, 4A). Sites where the fungus has entered the tips in both these genera are far less frequent, and there is little or no additional host wall material around the penetrating hyphae (Fig. 5C). The host cytoplasm in the majority of infected cells is electron dense and, in contrast to that in the healthy hyphae, appears to be necrotic (Fig. 5D). The rhizoid walls in both *Jungermannia* and *Nardia* are much thinner (less than 0.5 µm) than in the other genera (approximately 2 µm) and lack the mucilaginous stratum seen in *Cladopodiella* and *Calypogeia*. There is a marked tendency for the hyphae to grow over the outer surface of the rhizoids inside a thin layer of cuticle-like material (Fig. 5C).

Discussion

The experiments described here clearly demonstrate that liverwort rhizoidal ascomycetes, previously shown to have a wide host range and extending to the Ericaceae in the northern hemisphere (Duckett & Read, 1995), can also infect members of the Schistochilaceae from the southern hemisphere, where they induce branching and septation of the rhizoids mirroring that seen in natural associations (Pressel et al., 2008). Similarly, the fungal isolates from *Pachyschistochila* produce rhizoidal infections

indistinguishable from those found in nature in northern hemisphere liverworts and in *Calluna*.

These results are closely in line with expectation since sequencing of the fungi reveals that they all belong to the *Rhizoscyphus ericae* aggregate (Upson et al., 2007; Pressel et al., 2008; Bidartondo & Duckett, unpublished data). It is also noteworthy, in the context of wide host ranges, that the circumsubantarctic *Rhizoscyphus*-containing liverwort *Cephaloziella varians* (Upson et al., 2007), synonymous with *C. exiliflora* (Taylor) R. M. Schust. in the earlier study by Chambers et al. (1999), often grows in close proximity to the two *Pachyschistochila* species used in the present study (Engel, 1978).

However, since there is considerable genetic diversity within the *Rhizoscyphus ericae* aggregate, with only selected isolates forming ericoid and ectomycorrhizas (Vralstad et al., 2001), molecular studies are now needed to determine precisely which strains colonize liverworts in nature and whether these vary between taxa and across the geographical ranges of widely distributed species.

Given the present results, it would also seem likely that an ascomycete infection induces septation of the rhizoids in *Arachniopsis* and *Acromastigum* (Kitagawa & Kodama, 1974) in the Lepidoziaceae, most genera of which (e.g., *Chloranthelia*, *Hygrolembidium*, *Kurzia*, *Lepidozia*, *Megalembidium*, *Neogrollea*, *Pseudocephalozia*, *Psiloclada*, *Telaranea*, *Zoopsis*) possess ascomycete-containing rhizoids. Whether similar induction of rhizoid septation also applies to *Vetaforma*, in the putative sister family to the Lepicoleaceae (Crandall-Stotler & Stotler, 2000) that lacks fungi (Heinrichs et al., 2007), or to *Xenochila*, nested within the fungus-free Plagiochilaceae (Degenkolbe, 1938), is more problematic. The program of cytological and cross-infection studies should now be extended to include the swollen fungus-infected rhizoids of *Mylia anomala* (Duckett et al., 1991) and the Balantio-psidaceae (Duckett, unpublished data). These experiments should include *Xylaria*, identified from *Bazzania* (Davis et al., 2003), to establish whether this fungus can also form rhizoid associations in healthy rhizoids like those described here and other fungi, such as *Melionomyces*, related to *Rhizoscyphus* (Hambleton & Sigler, 2005).

The discovery that ascomycetes proliferate in the rhizoids of *Nardia scalaris* (Fig. 5C, D), whose stems contain a host-specific basidiomycete (Duckett et al., 2006a), requires molecular

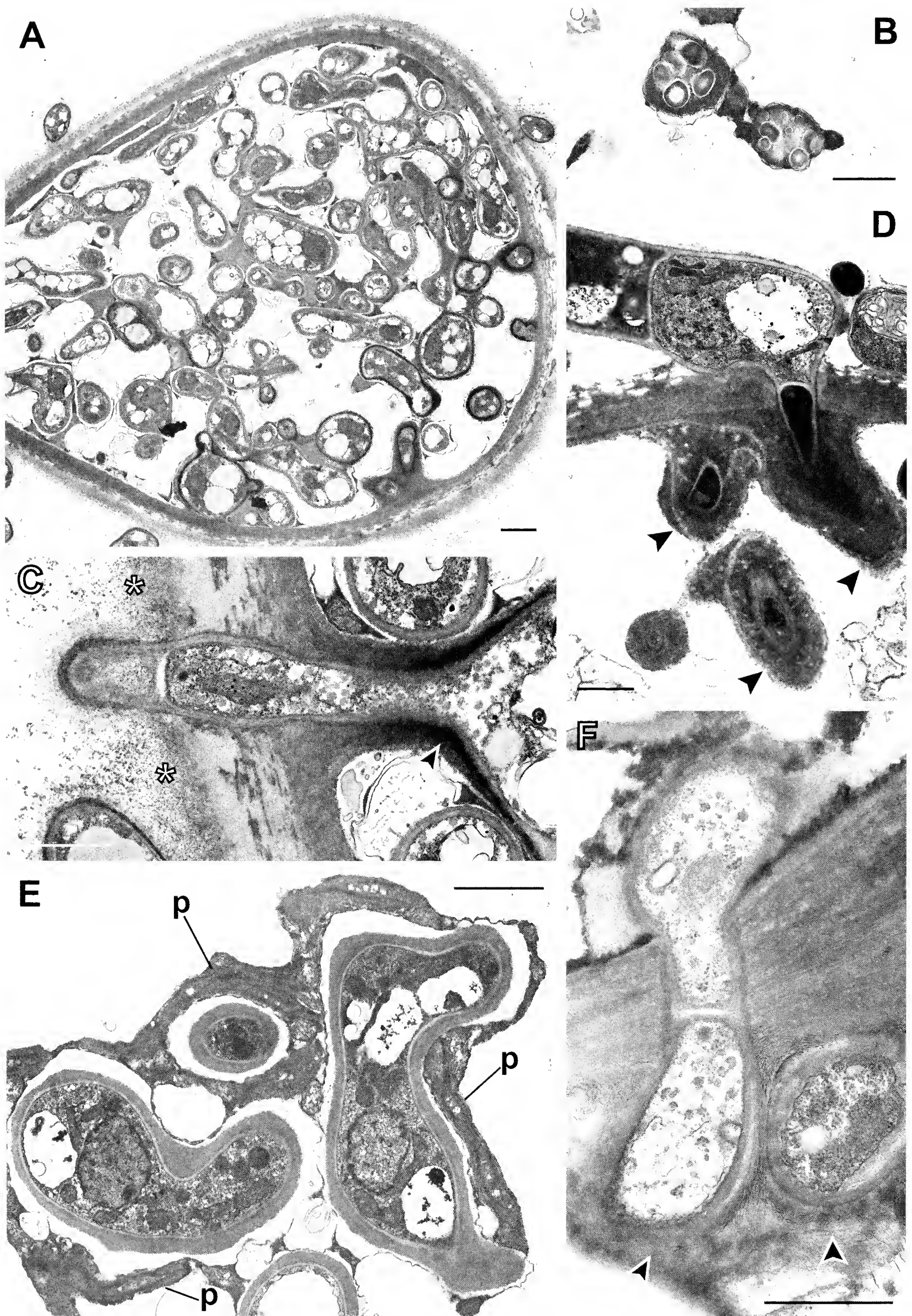


FIG. 4. (A–D) *Calypogeia fissa*, rhizoids infected with *Rhizoscyphus* from *Calluna*. (A) Rhizoid apex packed with hyphae. (B) Starch-filled plastids. (C) Hyphal penetration site. Note the mucilaginous outer wall layer (*) of the rhizoid and the collar of dense host wall material around the hypha (arrowed) inside the rhizoid. (D) Pegs of host wall material (arrowed) at the rhizoid base prevent the spread of the fungus into the host stem cells. (E) *Odontoschisma sphagni*, wild-infected rhizoid from a flagelliform axis showing elongate plastids (p) in the host cytoplasm adjacent to the hyphae. (F) *Calluna vulgaris*, wild mycorrhizal root showing fibrillar host wall material (arrowed) around the penetrating hypha. Scale bars: A, E = 2 μ m; B–D, F = 1 μ m.

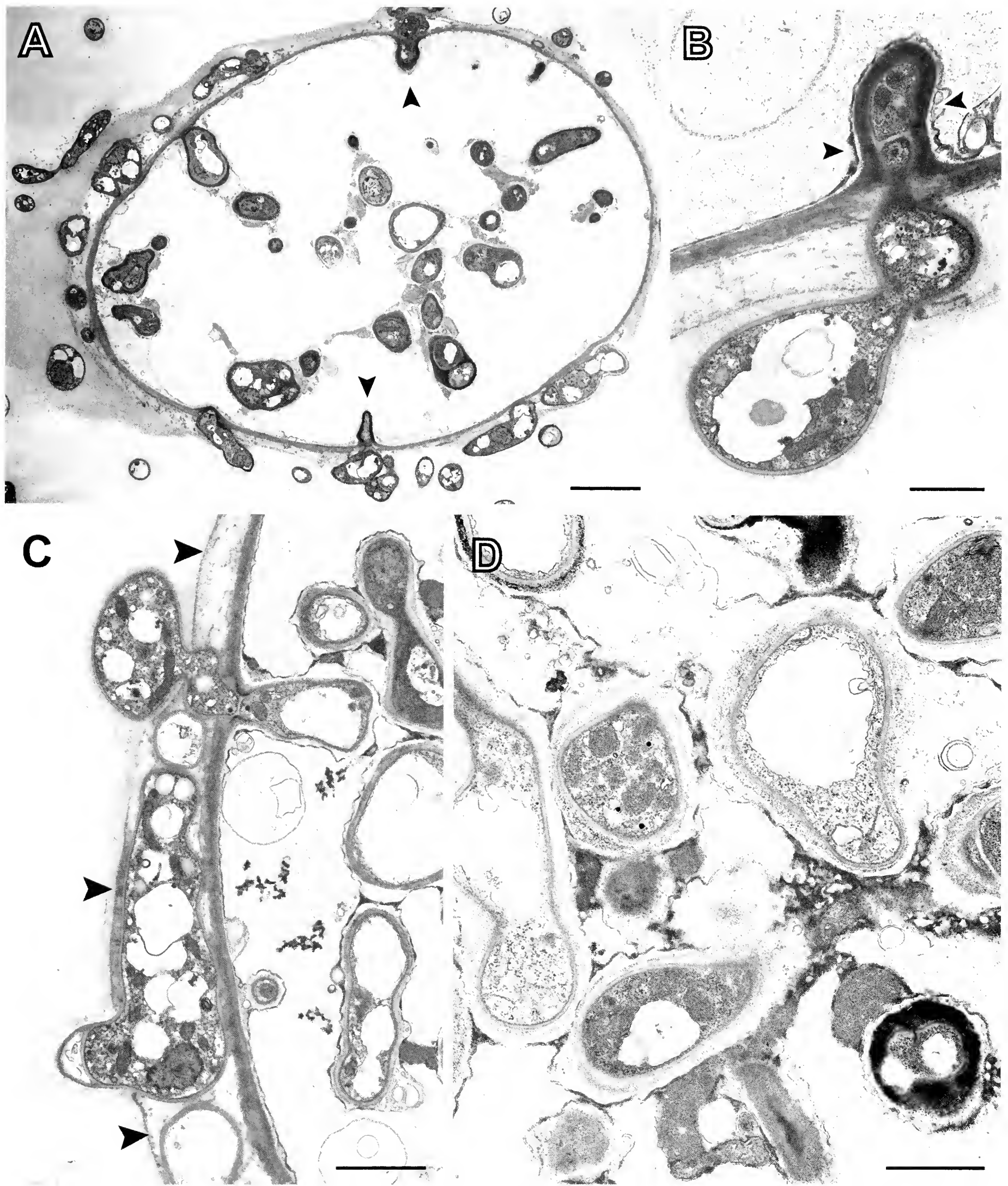


FIG. 5. Noncompatible rhizoid infections with *Rhizoscyphus*. (A, B) *Jungermannia gracillima*. (A) The swollen apex contains far fewer hyphae than in compatible infections (cf. Figs. 3B, 4A). Two points where hyphal ingress was prevented by overgrowths of host wall are arrowed. (B) Detail of host wall overgrowth (arrowed). (C, D) *Nardia scalaris*. (C) Hyphal penetration site; note the absence of additional host wall material and the hyphae lying between the rhizoid wall and the layer of cuticle-like material (arrowed). (D) Dense host cytoplasm around infecting hyphae. Scale bars: A = 5 μm ; C = 2 μm ; B, D = 1 μm .

studies to test the possibility that this liverwort naturally contains two fungal endophytes. In the previous cross-infection studies on *Nardia scalaris*, the basidiomycete was isolated from stems with all the rhizoids excised (Duckett et al., 2006a). Absence of hyphal proliferation and numerous failed penetration sites in *Jungermannia gracillima* rhizoids in culture, like those produced in mosses in response to pathogenic fungi (Martinez-Abigair et al., 2005), and the absence of fungal infected rhizoids in nature indicate that this liverwort, in common with other members of the genus (Duckett, unpublished data), does not form mycotrophic associations.

After the demonstration that liverwort ascomycetes can infect a wide range of host species, a second major finding from this study is the wide range of host rhizoid responses to *Rhizoscyphus ericae*. *Kurzia* and *Lepidozia*, in the Lepidoziaceae, produce swollen and often almost spherical rhizoid apices even in the absence of the fungus, whereas deformations of rhizoid tips occur only in the presence of a compatible fungus in the Cephaloziaceae and Cephaloziellaceae (Duckett et al., 1991; Duckett & Read, 1995). Rhizoid morphology remains largely unchanged following infections in *Bazzania* and *Odontoschisma*.

In most genera, hyphae proliferate in the rhizoid tips but form basal coils in *Odontoschisma* (Duckett et al., 1991). In the Cephaloziaceae and Calypogeiaceae, the fungal hyphae can penetrate the basal walls of rhizoids and form peg-like structures projecting into the adjoining parenchyma cells of the stem, but further development in the stem tissue appears to be stopped by the deposition of host wall material (Fig. 4D; see also Duckett et al., 1991). *Pachyschistochila* is the only documented instance of a liverwort where ascomycetous endophytes colonize a parenchyma tissue, although this is derived from the rhizoids (Pressel et al., 2008).

In ascomycete-infected rhizoids, the formerly ovoid nuclei move from a lateral (Fig. 1G) to a central location (Fig. 3I) and become highly pleomorphic just like those in basidiomycete-infected stem cells in other liverworts (Duckett et al., 2006a). An exception is *Pachyschistochila*, where the nuclei retain a compact spheroidal shape as in noninfected cells (Pressel et al., 2008). Also common to basidiomycete and ascomycete infections in leafy liverworts is healthy host cytoplasm with frequent dictyosomes. These are all features indicative of balanced mutualistic relationships unlike the necrotic rhizoid cytoplasm and sites

of failed fungal entry as observed in *Nardia* and *Jungermannia*.

Ingrowths of host wall are common to hyphal penetration sites for both ascomycetes and glomeromycote infections in thalloid liverworts (Ligrone et al., 2007). A labyrinthine interfacial matrix is so far unique to *Pachyschistochila* (Fig. 3C). A final source of intergeneric variation is the nature of the rhizoid walls. Their outer stratum is mucilaginous in *Cladopodiella* (Duckett et al., 1991) and *Odontoschisma* but not the other genera. *Cladopodiella* is the only example to date of the fungus forming a pseudoparenchymatous sheath in the mucilage around infected rhizoid tips associations. The intercellular phase of the glomeromycote infections in *Treubia* is similarly pseudoparenchymatous within mucilage-filled intercellular spaces inside the thallus (Duckett et al., 2006b).

Notwithstanding the wide fungus-host range, this suite of cytological differences point strongly toward the independent acquisition of ascomycete associations in liverworts on several occasions and frequent host swapping between them and members of the Ericales on acidic, nutrient-poor substrata, as has previously been suggested between glomeromycote associations in vascular plants, including pteridophytes, gymnosperms and flowering plants, and thallose liverworts (Read et al., 2000; Russell & Bulman, 2004; Selosse, 2005; Ligrone et al., 2007).

Although on cytological grounds multiple origin of the ascomycete associations in liverwort rhizoids seems highly probable, it is nevertheless interesting to consider their distribution overall within the Jungermanniidae. They are absent, as are other fungi, from the Porellales and first appear in the Schistochilaceae, the clade sister to all other members of the Jungermanniales (Davis, 2004, 2005; Forrest et al., 2006; Hentschel et al., 2006). Within the Jungermanniales, the much more widespread distribution of ascomycetes than basidiomycetes (Duckett et al., 2006a) strongly suggests they pre-dated the latter. The recent dating of the origins of the Schistochilaceae in the Triassic, over 250 million years ago (Heinrichs et al., 2007), suggests that their fungal association may have arisen long before the establishment of mycorrhizas in the Ericales, a group calculated to have arisen not more than 106 million to 114 million years ago (Wikström et al., 2001). The predominantly southern hemisphere/Gondwanaland distributions of most of the liverworts with ascomycetes also points to significant antiquity. It thus remains an open question: Did

the Ericales first acquire ascomycetes from the rhizoids of liverworts or vice versa? The patchy distribution of the ascomycete-containing liverworts in clades derived from the Schistochilaceae supports the cytological evidence for more recent origins and multiple instances of host swapping (Selosse, 2005).

Apart from sequencing studies to gather precise information on the identity of the ascomycetes in liverworts, an even bigger challenge for the future is to determine the functional significance. Although the cytology of the rhizoid-ascomycete associations points toward balanced relationships, with the fungi obtaining carbohydrates from their hosts, at present we have no clues as to the possible benefits to the liverworts since the growth and vigor of the resynthesized associations in the present and previous studies (Duckett & Read, 1995) was not notably different from that of the liverworts growing axenically. Most likely, this is because our culture medium contained more than sufficient nutrients to support active growth of the liverworts, all of which are from habitats extremely low in nutrients. Future experiments, under nutrient conditions that will limit growth of the liverworts, may provide clues as to the possible benefits from the presence of the fungus.

Since many of the ascomycete-containing liverworts grow together with members of the Ericales, it has been suggested that, aside from possible enhancement of nutrient availability and increased resistance to adverse effects of acidic peaty substrata by the presence of the fungus alone, the two plants might be interconnected in nature, thus opening the possibility of nutrient transfers via the common mycobiont (Duckett et al., 1991; Duckett & Read, 1995). Microcosm experiments like those demonstrating carbohydrate transfer from *Betula* to the parasitic liverwort *Cryptothallus* via their common basidiomycete fungus (Read et al., 2000; Bitardondo et al., 2003) should now be extended to the ascomycetous liverworts as emphasized by Selosse (2005).

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FIELDIANA

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Chapter Seven: Pattern of Leaf Development in Schistochilaceae Xiaolan He-Nygrén and Pirkko Harju

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Abstract

Early stages of leaf development were studied in *Schistochila appendiculata* (Hook.) Dumort. ex Trevis., *S. nobilis* (Hook.) Trevis., *Pachyschistochila subhyalina* (R. M. Schust.) R. M. Schust. & J. J. Engel, and *Gottschea conchophylla* (E. A. Hodgs. & Allison) Grolle & Zijlstra, using transverse microtome sections. Like other groups of leafy liverworts, all four species have apical cells with three cutting faces and two primary leaf initials from which bilobed leaves are initiated. Apical cell geometry and early patterns of merophyte development are the same for all taxa studied, including those without underleaves. The wing of the leaf develops very early, shortly after the leaf lobes begin to form. The initial sign of wing development is the outward expansion and protrusion of a row of cells along the keel and the basisopic or posterior margin of the ventral lobe. These cells undergo subsequent divisions so that transverse sections of the young leaves appear Y-shaped.

Introduction

Schistochilaceae encompasses the largest and most vigorous plants in leafy liverworts, and

offers numerous characters in its morphology for species delimitation (Schuster & Engel, 1977, 1985). Among these morphological characters, the complicate-bilobed, winged leaf has been

considered as one of the characteristics of the family. The line of attachment of the dorsal lobe to the commonly larger ventral lobe is subtended by laminal tissue that is confluent with the lamina of the ventral lobe. This tissue has been called the wing, and is considered to have originated from the keel and ventral lobe and to be part of it (see Schuster & Engel, 1977, 1985). Consequently, in current taxonomic studies, the width of the ventral lobe has been measured as the width of both the ventral lobe and the wing. The peculiar setting of the dorsal lobe of the lateral leaf led us to investigate early stages of leaf development in the family in order to evaluate its structure and morphology.

Materials and Methods

Species used as the representatives of the family for this study are *Schistochila appendiculata* (Hook.) Dumort. ex Trevis., *S. nobilis* (Hook.) Trevis., *Pachyschistochila subhyalina* (R. M. Schust.) R. M. Schust. & J. J. Engel, and *Gottschea conchophylla* (E. A. Hodgs. & Allison) Grolle & Zijlstra. The remaining genus of the family, *Pleurocladopsis* R. M. Schust., was not included in the study, but unlike the complicate-bilobed and winged leaf presented in other genera, it has a shallowly and equally bilobed and wingless leaf. All materials studied are from dried herbarium collections.

Sectioning

In order to observe the apical cell and the pattern of early leaf development, transverse microtome sections of the shoot apex were made. Paraffin embedding and sectioning were prepared using the following procedure. The samples were first moistened with water and then dehydrated with ethanol using the following concentrations in a graded series: 50%, 70%, 94%, and 100%; samples were incubated in each of the first three dilutions for 1–2 hours, and then in 100% ethanol overnight. For paraffin embedding, the samples were transferred into an intermediate solvent 1-Butanol in graded solutions (2:1 100% EtOH and 1-Butanol, 1:2 100% EtOH and 1-Butanol, and 1-Butanol) at 1–2 hour intervals. Then the samples were left overnight in the 1-Butanol solution with added Erythrosin B. The samples were then transferred into tubes with 1 ml

1-Butanol, and the tubes were filled with 9 ml melted paraffin. Extra paraffin was added when the 1-Butanol evaporated. The tubes were placed in a paraffin oven at 58°C for at least a week. The samples were sectioned with a Leica RM2165 rotary microtome, at a thickness of 10 µm. The sections were mounted on glass slides and stained using standard Safranin methods (see Ruzin, 1999).

Specimens used for microtome sectioning and photographing

Schistochila appendiculata. New Zealand, South Westland, near Lake Matheson, February 2007, *He-Nygrén* 2269 (H).

Schistochila nobilis. New Zealand, South Island, Lewis Pass, along track from St. James Walkway to Cannibal Gorge, February 2007, *He-Nygrén* 2176 (H).

Pachyschistochila subhyalina. New Zealand, South Westland, Moeraki Valley Track, October 2001, *Glenny* 8529 (H).

Gottschea conchophylla. New Zealand, Arthur's Pass, Mt. Aiken, September 2001, *Glenny* 8496 (H).

Results

Apical cell and merophyte

All four species studied have their apical cells with three cutting faces: two lateral and one ventral. The apical cells undergo divisions that are parallel to the cutting faces and these segments are cut off in a spiral sequence. The ventral cutting face of the apical cell and its two corresponding lateral cutting faces in all four species are of equal size (Fig. 1). Also, comparing merophytes of similar age, there is no difference in how much they each contribute to the stem. The ventral merophytes differ only in leaf development. In *Gottschea*, underleaves do not develop, but the stem tissue can still develop equally from lateral and ventral merophytes.

Leaf development

At early stages of development bilobed leaves initiated from two primary leaf initials can be traced in all species investigated. The pattern of

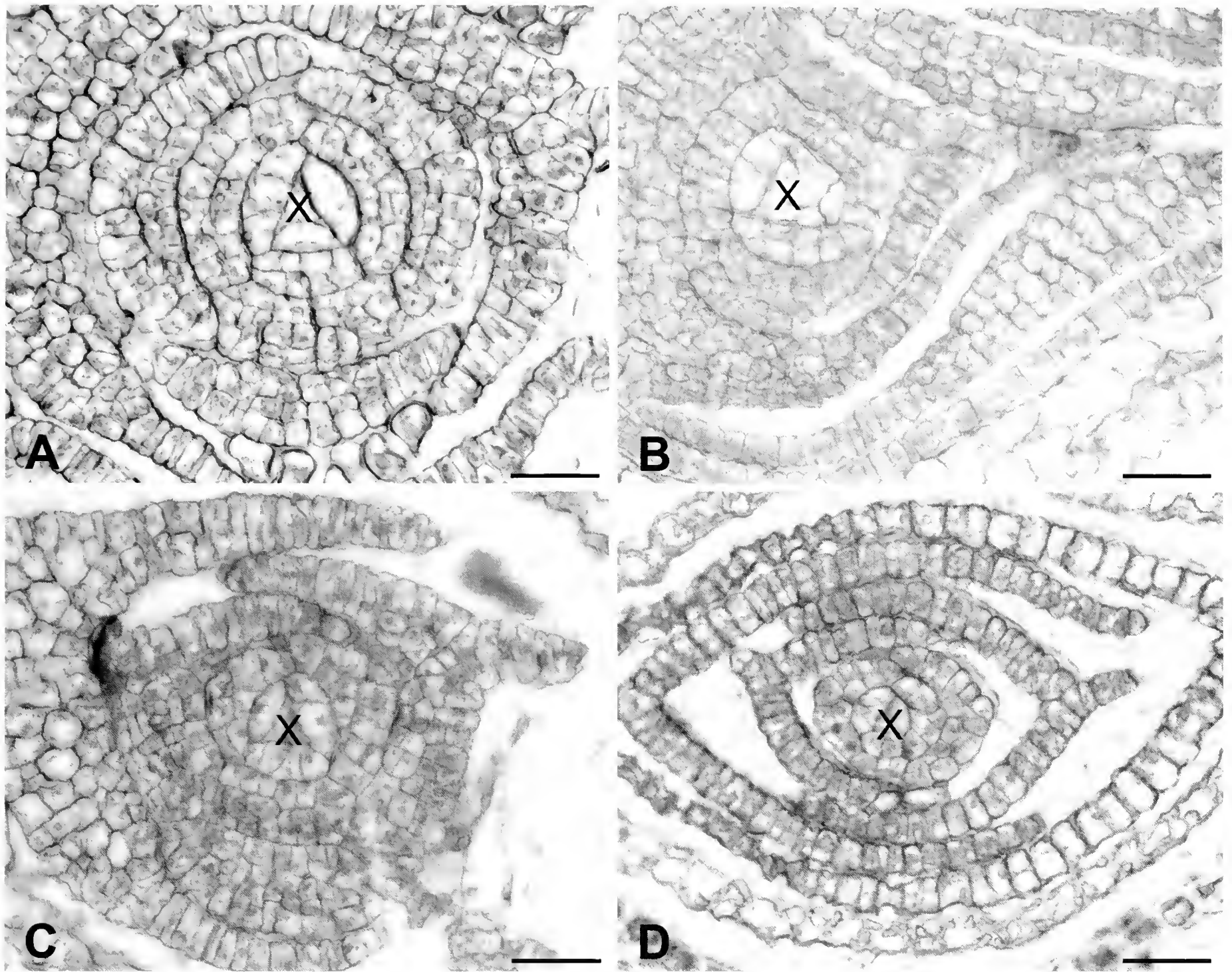


FIG. 1. Transverse section through the stem or branch apex showing the apical cell; x = apical cell; bar lines = 50 μ m. A: *Schistochila appendiculata*, B: *Schistochila nobilis* (through branch apex), C: *Pachyschistochila subhyalina*, D: *Gottschea conchophylla*.

wing origin and leaf development is similar in all four species. Examination of the early divisions of the lateral merophytes next to the apical cells (Fig. 1A, C, and D), suggests that the first division is not truly equal, but instead forms a somewhat smaller dorsal cell. The wing of the leaf has developed very early in leaf ontogeny, shortly after the leaf lobes begin to form. In Fig. 2A, the section of the leaf was taken at the point where the sinus between dorsal and ventral lobes begins and the single wing is confluent with the ventral lobe. Sections B–D of Fig. 2 progress down the leaf toward its point of insertion on the stem. In these views, the wing is only 1 cell broad and appears to project from the keel. Our result shows that the wing forms from a row of cells that protrude from the keel and continue distally along the basisopic or posterior margin of the ventral lobe. These cells undergo subsequent divisions so that transverse sections of the young leaves

appear Y-shaped. In Fig. 2A, the abaxial surface of the underleaf has two lamellae forming on it, as is common in *Schistochila appendiculata*. The additional lamellae can also occur on the distal, abaxial surface of the ventral lobe of the leaf (not shown here). However, these structures are not homologous to the wings formed from cells of the keel and posterior margin of the ventral lobe.

Discussion

The form of the plant is the result of the process of development of merophytes cut off by the apical cell. Like most of the leafy liverworts, the apical cell in Schistochilaceae lies with one cutting face toward the ventral side and two toward the lateral side. In this study we confirm the earlier study by Goebel (1930) in showing that the wings

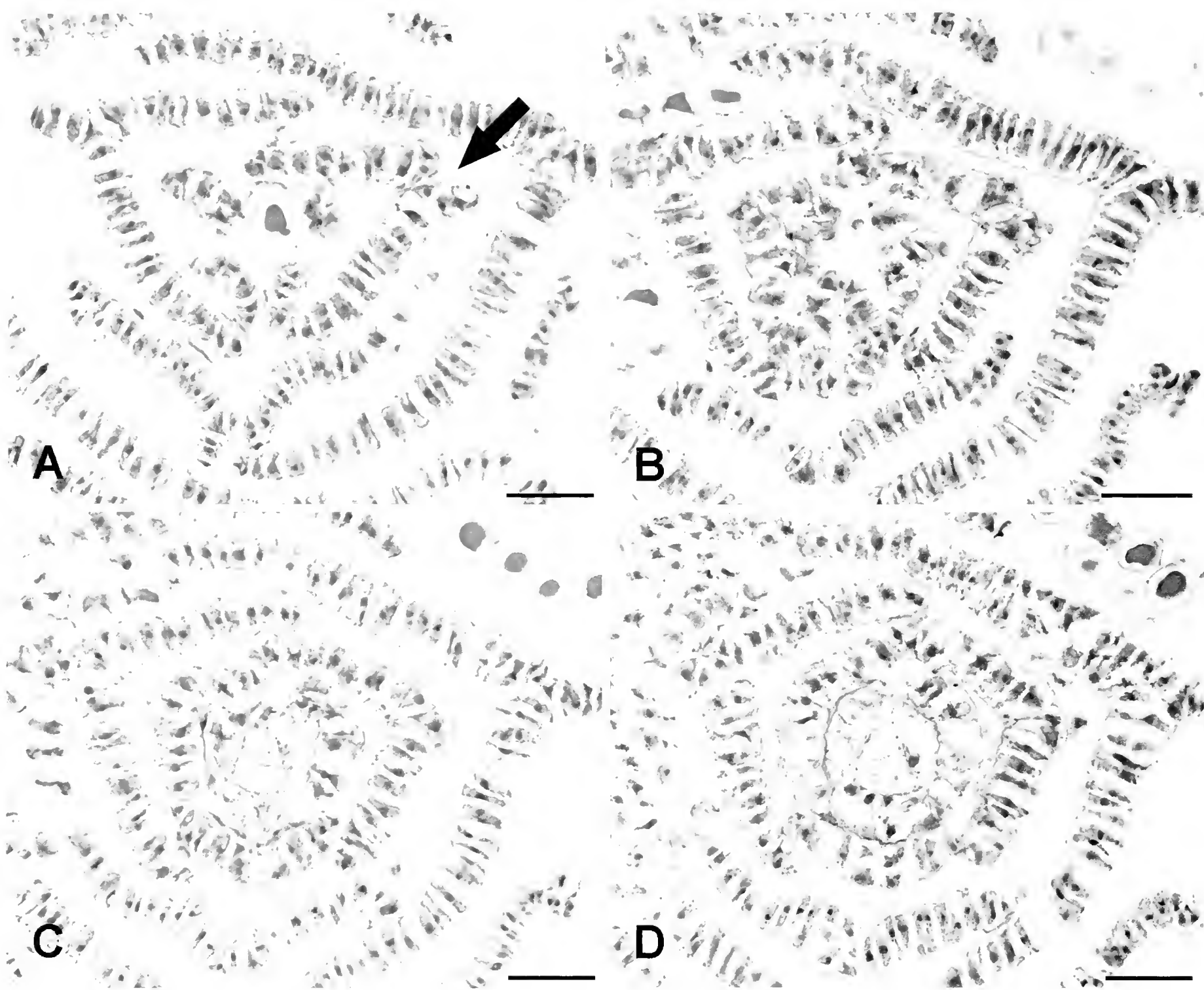


FIG. 2. A series of transverse sections A–D showing that the wings develop early from the keel and posterior margin of the ventral lobe. Section A is cut just above the apical cell and the others proceeding down into the stem by 30 μm (D is the deepest into the stem). The arrow in A points to the wing, at the point of the sinus between the dorsal and ventral lobes and is confluent with the ventral lobe; bar lines = 50 μm . Species, *Schistochila appendiculata*.

develop early from the keel and posterior margin of the ventral lobe in all of the species studied. Apical cell geometry and early patterns of merophyte development are the same for all taxa studied, including those without underleaves. In Schistochilaceae, species having an incubous leaf insertion and lack of underleaves belong to the genus *Gottschea* Nees ex Mont., however, some authors have rejected this genus based on the presence of bracteoles on gynoecia (e.g., Piippo, 1984; So, 2003a, 2003b). However, some authors have rejected this arrangement based on the presence of bracteoles on gynoecia (e.g., Piippo, 1984; So, 2003a, 2003b). Our study shows that the early leaf ontogeny of *Gottschea* is the same as that of *Schistochila*, so this result suggests that there is a need to further study the phylogenetic relationship of the two groups. Possibly the differences in

mature plants between the two genera are induced by ecological and environmental factors.

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Part Four: Liverwort Anatomy and Cytology

Chapter Eight: Karyological Studies on Some Liverworts from China and Singapore

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Abstract

Karyological observations were made on 14 species of liverworts from China and Singapore. The chromosome numbers of four species, *Metzgeria consanguinea* Schiffn. ($n=8$), *Riccardia elata* (Steph.) Schiffn. ($n=9+m$), *Riccardia graeffei* (Steph.) Hewson ($n=9+m$), and *Riccardia kodamae* Mizut. & S.Hatt. ($n=9+m$), are reported for the first time. The karyotype formulae of *Riccardia elata*, *Metacalypogeia cordifolia* (Steph.) Inoue ($n=9$), *Pallavicinia lyellii* (Hook.) Carruth. ($n=8$), *Pellia epiphylla* (L.) Corda ($n=8+m$), and *Scapania ciliata* Sande Lac. ($n=8+m$) are provided. Two different chromosome numbers ($n=9$, $n=9+m$) were found in *Jubula javanica* Steph. Of 14 species investigated cytologically, eight species have an m-chromosome. *Riccardia elata* is new to the liverwort flora of China.

Introduction

The bryophytes form the second largest group of green land plants after the flowering plants. The group is recently classified into three divisions: Marchantiophyta (liverworts), Bryophyta (mosses), and Anthocerotophyta (hornworts) (Zhu et al., 2006). Liverworts are considered to be the earliest land plants (Qiu et al., 1998). The cytology of liverworts, however, is poorly known, especially in China and Singapore (Zhu et al., 2002; Zheng et al., 2005). The present paper reports the chromosome numbers of 14 liverwort species from China and Singapore.

Materials and Methods

Materials for the cytological study were collected in China and Singapore in 2003–2007. Most of them were pretreated and fixed directly in the field. Some fresh samples were brought to the laboratory in plastic bags, and transferred to a CLMACELL for further culture at 15°C and ca. 4,500 LUX with a regime of 12 hour light and 12 hour dark. The tips of living shoots were cut off and placed in saturated p-Dichlorobenzene for 3–5 hours, then fixed in Carnoy's fluid (ethanol: acetic acid=3:1) at room temperature for 24 hours. After fixation, the tips were kept in 70% ethanol at ca. 4°C. The above treated materials were transferred in 50% ethanol for 5 minutes, then washed with distilled water. After thorough washing, the materials were hydrolyzed in 1N HCl at 60°C for 5 minutes, followed by soaking in distilled water for 10 minutes. The materials were dissected with two fine needles under a stereomicroscope and stained in carbol fuchsin at room temperature and then squashed softly. Photographs of chromosomes were made with an Olympus microscope (BX51) and a digital CCD Color Camera Kit (Evolution™ MP). Drawings were made with the aid of an Olympus drawing tube. The methods for representation of karyotypes and karyotypic analysis are the same as those described in Ramsay (1982) and Inoue et al. (1994). Five or more chromosome plates per species were measured.

Results and Discussion

An alphabetical listing of the species that we investigated is presented below. The mean length

and width of the largest chromosome (L), the smallest one (S), and m-chromosome (if present) in metaphases are given in the parenthesis after the chromosome number.

Herbertus dicranus (Taylor ex Gottsche et al.) Trevis. (Fig. 1A)

CYTOLOGY— $n=9$ (L: $3.60 \times 0.60 \mu\text{m}$; S: $1.60 \times 0.60 \mu\text{m}$).

Our result ($n=9$) confirms the earlier report of Tatuno (1947, 1948) on the Taiwanese samples of *Herbertus longifolius* Horik. The cytotype of this species includes four larger V-shaped chromosomes, three median ones, and two smaller ones (Fig. 1A).

VOUCHER SPECIMEN—CHINA. ZHEJIANG: Fengyangshan Nature Reserve, 1300 m, on rocks, 29 July 2006, R.-L. Zhu et al. 2006072903 (HSNU).

Jubula javanica Steph. (Fig. 1B–E)

CYTOLOGY— $n=9$ (L: $1.60 \times 0.45 \mu\text{m}$; S: $0.45 \times 0.40 \mu\text{m}$); $n=9+m$ (L: $1.80 \times 0.50 \mu\text{m}$; S: $0.50 \times 0.40 \mu\text{m}$; m: $0.20 \times 0.20 \mu\text{m}$).

Two Chinese populations of *Jubula javanica* were examined for the chromosome number. Chromosome number ($n=9$) was counted in most metaphases (Fig. 1B–C), but $n=10$ ($9+m$) was seen in four cells of one population (Zhu et al. 2005090206) (Fig. 1D–E). The previous reports for chromosome numbers $n=9$ of this species were based on the materials from Japan (Tatuno, 1938a, 1941a, 1941b; Tatuno & Nagatomo, 1969; Guerke, 1978) and Taiwan (Tatuno, 1948).

VOUCHER SPECIMENS—CHINA. HAINAN: Bawangling Nature Reserve, 1150 m, on rock in water, 660 m, 29 November 2003, R.-L. Zhu et al. 2003112902 (HSNU); CHINA. HAINAN, Diaoluoshan Nature Reserve, on tree trunk, 990 m, R.-L. Zhu et al. 2005090206 (HSNU).

Metacalypogeia cordifolia (Steph.) Inoue (Fig. 1F–G)

CYTOLOGY— $n=9$ (L: $3.53 \times 0.88 \mu\text{m}$; S: $0.93 \times 0.66 \mu\text{m}$).

The chromosome number of this species from the Chinese material is the same as the earlier report based on Japanese samples (Inoue, 1967) (Fig. 1F–G), but the karyotype formula of this species ($K[n]=9=6V+3v$) is different from Inoue's (1967) report ($K[n]=9=H+4V+3J+h$).

VOUCHER SPECIMEN—CHINA. ZHEJIANG: Fengyangshan Nature Reserve, 1510 m, on rocks, 30 July 2006, R.-L. Zhu et al. 2006073008 (HSNU).

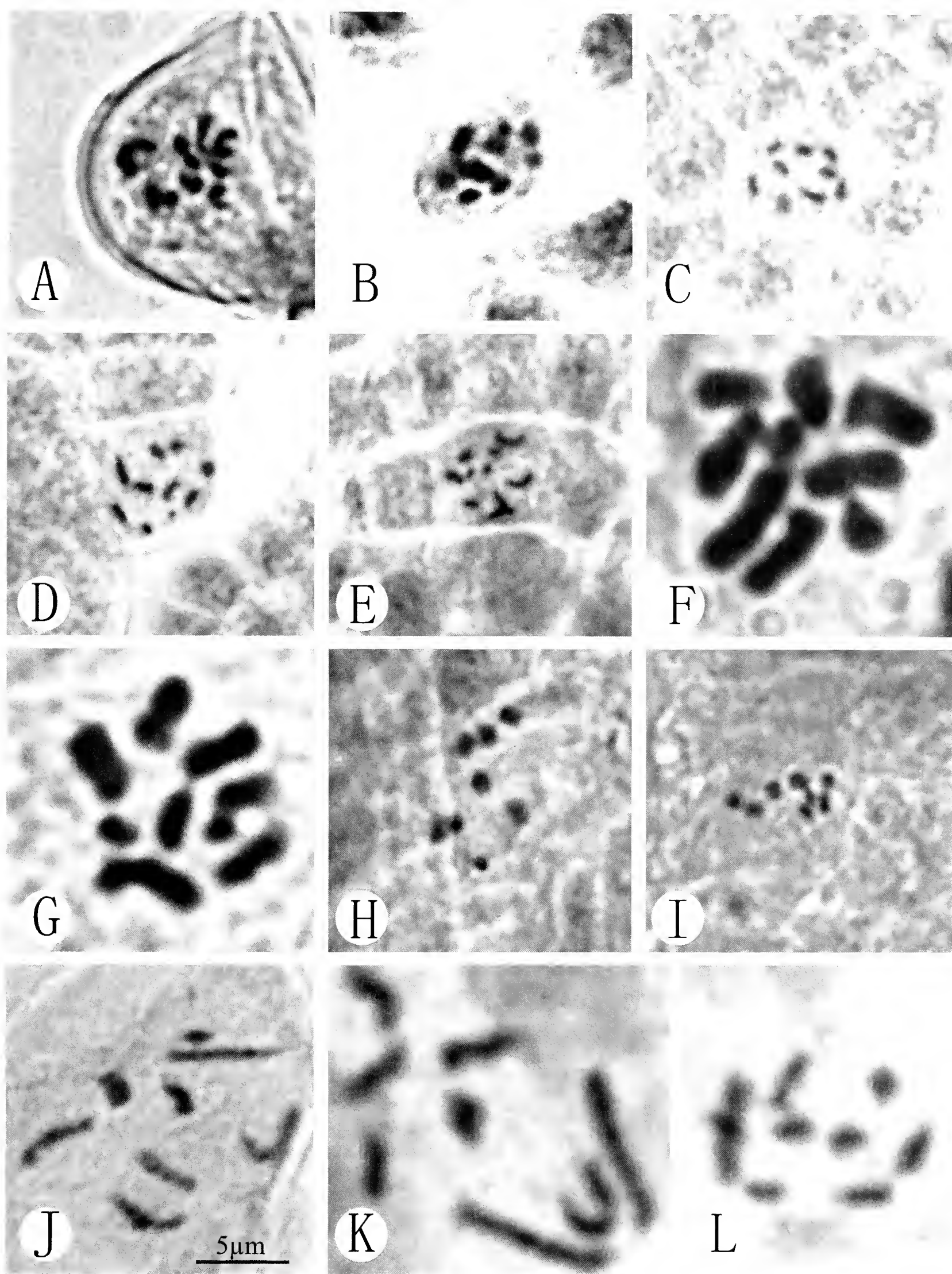


FIG. 1. Photomicrographs of mitotic metaphase chromosomes in gametophytes of some liverworts. (A) *Herbertus dicranus*, $n=9$. (B, C) *Jubula javanica*, $n=9$. (D, E) *Jubula javanica*, $n=9+m$. (F, G) *Metacalypogeia cordifolia*, $n=9$. (H–J) *Metzgeria consanguinea*, $n=8$. (K) *Metzgeria furcata*, $n=8+m$. (L) *Monosolenium tenerum*, $n=9$.

***Metzgeria consanguinea* Schiffn. (Fig. 1H–J)**

CYTOLOGY— $n=8$ (L: $1.26 \times 0.71 \mu\text{m}$; S: $0.71 \times 0.54 \mu\text{m}$).

This is first report of the chromosome number of this species. Two different cytotypes were

found. The first cytotype consists of eight small chromosomes (Fig. 1H–I). It is difficult to identify centromeres during metaphase in this species just as in *Frullania* (Iverson, 1963). However, we also found the second cytotype

consisting of five large ($3V + 2J$) chromosomes, two median ones ($j + v$), and an m-chromosome (Fig. 1: J). The largest chromosome of the second cytotype is much larger than that of the first cytotype, as shown in Fig. 1H–J.

VOUCHER SPECIMEN—CHINA. GUANGXI: Maoershan Nature Reserve, 2100 m, on tree trunks, 3 September 2004, *R.-L. Zhu et al.* 20049301 (HSNU).

***Metzgeria furcata* (L.) Dumort. (Fig. 1K)**

CYTOLOGY— $n = 8 + m$ (L: $4.10 \times 0.40 \mu\text{m}$; S: $1.50 \times 0.50 \mu\text{m}$; m: $0.70 \times 0.50 \mu\text{m}$).

In this widespread species, three different chromosome numbers ($n = 8$, $n = 8-10$, $n = 9$) have been reported (Fritsch, 1991). Our counts confirmed the same number $n = 9$ (including an m-chromosome) (Fig. 1K) as reported by Kuta et al. (1990) from the material of Poland. The chromosomes of this species are larger than those of the first cytotype of *Metzgeria consanguinea* except the m-chromosome (Fig. 1H, I, K).

VOUCHER SPECIMEN—CHINA. ZHEJIANG: Fengyangshan Nature Reserve, 1450 m, on tree trunks, 30 July 2006, *R.-L. Zhu et al.* 2006073001 (HSNU).

***Monosolenium tenerum* Griff. (Fig. 1L)**

CYTOLOGY— $n = 9$ (L: $1.60 \times 0.40 \mu\text{m}$; S: $0.70 \times 0.40 \mu\text{m}$).

The chromosome number of this species is $n = 9$ and the cytotype includes one larger chromosome and eight median ones (Fig. 1L). Our results confirmed the previous reports given by Tatuno (1955, 1957), based on the Japanese material (Fritsch, 1991).

Monosolenium tenerum is one of garden species previously called as “*Pellia endiviifolia*” (Gradstein et al., 2003). It is newly found in East China.

VOUCHER SPECIMEN—CHINA. SHANGHAI: Shanghai Botanical Garden, 4 m, on soil, 21 July 2006, *R.-L. Zhu* 20060721-1 (HSNU).

***Pallavicinia lyellii* (Hook.) Carruth. (Fig. 2A)**

CYTOLOGY— $n = 8$ (L: $15.29 \times 1.57 \mu\text{m}$; S: $5.57 \times 1.71 \mu\text{m}$).

The chromosome number of *Pallavicinia lyellii* from two populations of China and Singapore is $n = 8$. The karyotype formula of the Chinese population is $K(n) = 8 = 3V + 4J + v$. Most earlier reports showed the same number $n = 8$ of this species from China (Taiwan), Japan, Peru, and United States (Fritsch, 1991), but Wolcott (1940) reported the chromosome number $n = 9$ from

the North Carolina and Texas. The chromosome number $n = 9$ and $n = 18$ were also found in the material from Texas (Wolcott, 1941).

VOUCHER SPECIMENS—CHINA. HAINAN: Bawangling Nature Reserve, 1150 m, on dead wood, 27 November 2003, *R.-L. Zhu et al.* 2003112703 (HSNU); SINGAPORE. BUKIT TIMAH: Fern Valley, on soil, 3 February 2007, *R.-L. Zhu* 20070203-10 (♂, HSNU).

***Pellia epiphylla* (L.) Corda (Fig. 2B–D)**

CYTOLOGY— $n = 8 + m$ (L: $8.10 \times 0.86 \mu\text{m}$; S: $2.97 \times 0.94 \mu\text{m}$; m: $1.62 \times 0.90 \mu\text{m}$).

The chromosome number of this species is $n = 9$, including an m-chromosome. The karyotype formula is $K(n) = 9 = 3V + J + v + 3j + m$. The species has been studied cytologically many times (Fritsch, 1991). The number $n = 9$ and $2n = 18$ were repetitively confirmed since the early 20th century (Fritsch, 1991; Fuchs et al., 1995). Our results also showed the chromosome number $n = 9$.

VOUCHER SPECIMEN—CHINA. HAINAN: Bawangling Nature Reserve, 1150 m, on dead wood, 27 November 2003, *R.-L. Zhu et al.* 20050211-3 (HSNU).

***Riccardia elata* (Steph.) Schiffn. (Fig. 2E)**

CYTOLOGY— $n = 9 + m$ (L: $2.93 \times 0.66 \mu\text{m}$; S: $1.60 \times 0.40 \mu\text{m}$; m: $0.73 \times 0.60 \mu\text{m}$).

The chromosome number $n = 10$ of *Riccardia elata* is the same as most members of the genus *Riccardia*. This is the first report for chromosome number of this species. The karyotype formula is $K(n) = 10 = 4V + 5J + m$. *Riccardia elata* was known previously from Java, Singapore, the Philippines, and Vanuatu (Furuki, 2002, 2006). It is reported for China for the first time.

VOUCHER SPECIMEN—CHINA. HAINAN: Diaoluoshan Nature Reserve, 1060 m, on rocks, 4 September 2005, *R.-L. Zhu et al.* 2005090406 (HSNU).

***Riccardia graeffei* (Steph.) Hewson (Fig. 2F)**

CYTOLOGY— $n = 9 + m$ (L: $6.00 \times 0.80 \mu\text{m}$; S: $2.00 \times 1.00 \mu\text{m}$; m: $1.50 \times 1.20 \mu\text{m}$).

The chromosome number of *Riccardia graeffei* is $n = 10$. The cytotype is composed of five large chromosomes, four median ones, and one smaller one. The mean length of the chromosomes of this species is the largest among four *Riccardia* species investigated here. The largest chromosome is V-shape and about $6.00 \mu\text{m}$ long in mitotic metaphase. The chromosome number of this species is reported for the first time.

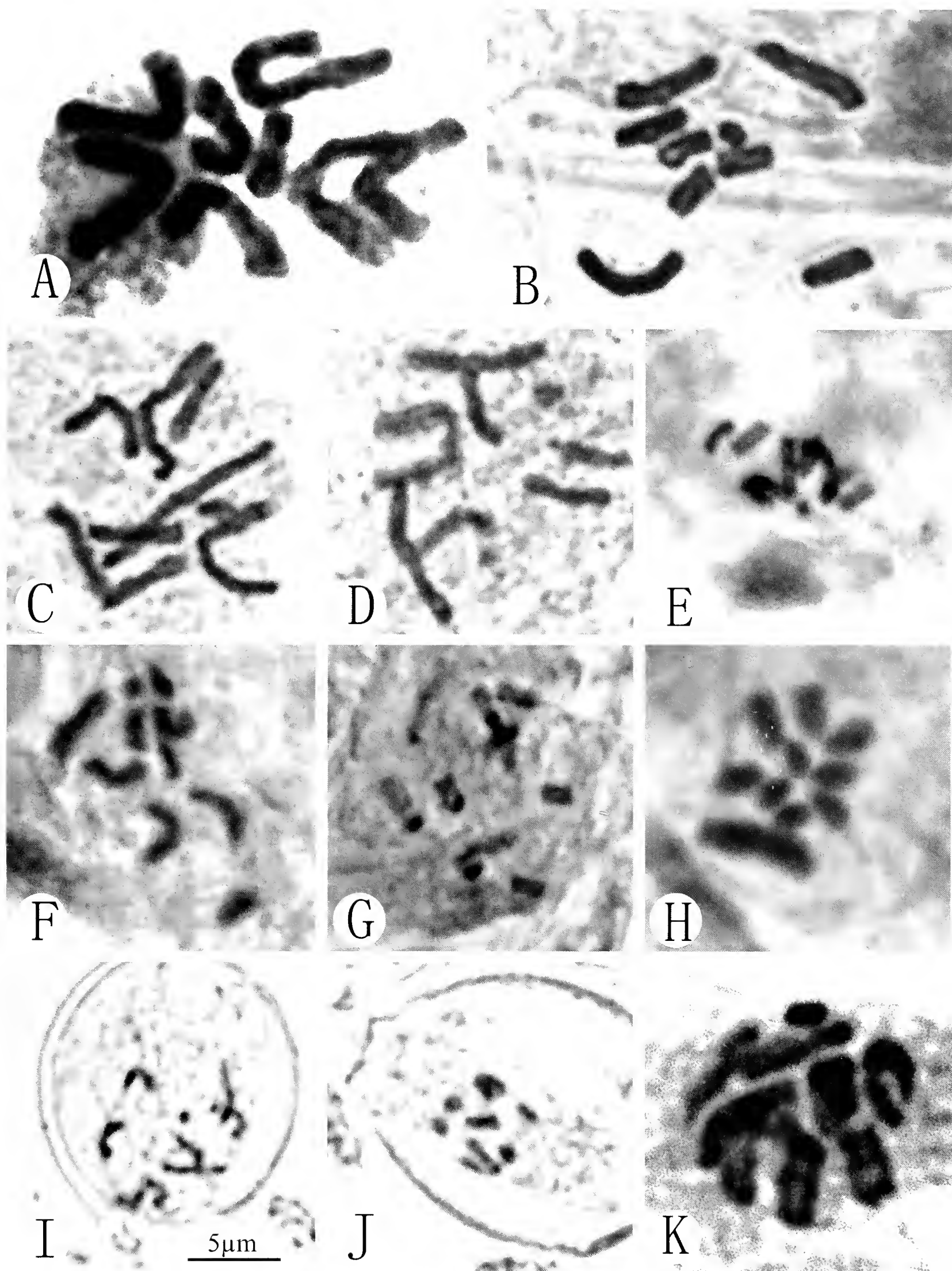


FIG. 2. Photomicrographs of mitotic metaphase chromosomes in gametophytes of some liverworts. (A) *Pallavicinia lyellii*, $n=8$. (B–D) *Pellia epiphylla*, $n=8+m$. (E) *Riccardia elata*, $n=9+m$. (F) *Riccardia graeffei*, $n=9+m$. (G) *Riccardia kodanue*, $n=9+m$. (H) *Riccardia uultifida*, $n=9+m$. (I, J) *Scapania ciliata*, $n=8+m$. (K) *Trichocolea tomentella*, $n=8+m$.

VOUCHER SPECIMEN—SINGAPORE. Bukit Timah: Fern Valley, on soil, 3 February 2007, R.-L. Zhu 20070203-6 (HSNU).

Riccardia kodamae Mizut. & S.Hatt. (Fig. 2G)

CYTOLOGY— $n=9+m$ (L: $3.70 \times 0.60 \mu\text{m}$; S: $0.90 \times 0.50 \mu\text{m}$; m: $0.70 \times 0.40 \mu\text{m}$).

The chromosome count of *Riccardia kodamae* is $n=10$, including an m-chromosome. The cytotype consists of four large, V-shaped chromosomes, five median ones, and an m-chromosome. This is the first report of the chromosome number of this species.

VOUCHER SPECIMEN—CHINA. ZHEJIANG: Tianmushan Nature Reserve, 900 m, on wet soil by river, 27 April 2006, R.-L. Zhu 2006042701 (HSNU).

Riccardia multifida (L.) Gray (Fig. 2H)

CYTOLOGY— $n=9+m$ (L: $4.67 \times 0.51 \mu\text{m}$; S: $1.47 \times 0.40 \mu\text{m}$; m: $0.80 \times 0.40 \mu\text{m}$).

The chromosome number of *Riccardia multifida* from the Chinese population is $n=10$. The cytotype of this species consists of one large chromosome, six median ones, and three smaller ones. The largest, V-shaped chromosome ranges from $3.2 \mu\text{m}$ to $7.6 \mu\text{m}$ in the mitotic metaphase of this species.

Intraspecific polyploidy in this species was found by several workers (Fritsch, 1991). Tatuno reported the chromosome number $n=10$ of several populations from Japan (Tatuno, 1938b, 1941a, 1941b). Newton (1971) reported $n=\text{ca. } 19$ by mitotic counts from Great Britain. The chromosome number $n=20$ was found in the European and Japanese materials (Lorbeer, 1934; Segawa, 1971; Meenks, 1981).

VOUCHER SPECIMEN—CHINA. ZHEJIANG: Fengyangshan Nature Reserve, 1300 m, on rocks, 30 July 2006, R.-L. Zhu et al. 2006073017 (HSNU).

Scapania ciliata Sande Lac. (Fig. 2I–J)

CYTOLOGY— $n=8+m$ (L: $2.81 \times 0.51 \mu\text{m}$; S: $1.89 \times 0.60 \mu\text{m}$; m: $0.70 \times 0.49 \mu\text{m}$).

The gemmae at tips of the leaves of *Scapania ciliata* were investigated cytologically. The chromosome number is $n=9$, including an m-chromosome. The karyotype formula of this species is $K(n)=9=7J+V+m$. This species was cytologically studied by Segawa (1965, as *Scapania spinosa* Steph.), Inoue (1977), and Sha et al. (2003), based on Japanese and Chinese material.

VOUCHER SPECIMEN—CHINA. GUANGXI: Maoershan Nature Reserve, 2100 m, on rocks,

3 September 2004, R.-L. Zhu et al. 20049304 (HSNU).

Trichocolea tomentella (Ehrh.) Dumort. (Fig. 2K)

CYTOLOGY— $n=8+m$ (L: $4.00 \times 1.20 \mu\text{m}$; S: $2.10 \times 1.00 \mu\text{m}$; m: $0.92 \times 0.80 \mu\text{m}$).

The chromosome number of this species is $n=9$, including an m-chromosome. The earlier records of this species showed the chromosome number $n=8+m$ or $n=9$ from Caucasus, China (Taiwan), France, Great Britain, Japan, and Poland (cf. Fritsch 1991). Du et al. (1997) also counted the same chromosome number $n=9$ from the populations collected from Sichuan province, China.

VOUCHER SPECIMEN—CHINA. HAINAN: Bawangling Nature Reserve, 1050 m, on dead wood, 28 November 2003, R.-L. Zhu et al. 2003112803 (HSNU).

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Abstract

Liverworts (Marchantiophyta) form a conspicuous and important component in many terrestrial ecosystems throughout the world. Despite of their significance and abundance, studies of various aspects on global plant species richness and distribution patterns have almost exclusively focused on vascular plants. Yet, comprehensive studies of liverwort plant diversity have many implications and broad applications. We use a preliminary dataset that unites liverwort nomenclature, taxonomy, and geography based on some 60,000 records. Global maps are produced for the taxonomic ranks of species, genus, and family to provide a rapid guide of diversity across political units worldwide. The usefulness of higher level taxon analyses was investigated at the genus and family level to test the relationship with species richness. A reduced set of taxonomic ranks other than species has been proved to be useful for rapid and cost-effective assessment of biodiversity. We provide the first examination of how well this method performs for liverworts. Generic richness was slightly more accurately related to species richness than that of families, indicating surrogacy at this taxonomic level as a promising

approach for the prediction of liverwort species richness. Finally, given the fact that vascular plant diversity and distribution patterns are often given high consideration in evaluating global networks of protected areas and biodiversity hotspots, we present a comparison of centers of species richness between liverworts and vascular plants. Several regions of high liverwort species richness lie outside the highest centers of vascular plant species richness. We conclude with ideas for future studies of the dataset, which has many exciting implications and applications for the study of liverwort distribution and diversity patterns.

Introduction

Knowledge of the spatial distribution of biodiversity is also crucial for its further exploration, use, and conservation (Mutke & Barthlott, 2005). Recently, there has been a growing number of studies documenting broad-scale patterns for many major groups of organisms, including vascular plants (Scotland & Wortley, 2003; Barthlott et al., 2005; Kier et al., 2005; Mutke & Barthlott, 2005; Kreft & Jetz, 2007), macrofungi (Mueller et al., 2007), mammals (Ceballos et al., 2005; Ceballos & Ehrlich, 2006), birds (Rangel & Diniz-Filho, 2004; Orme et al., 2005), amphibians (Wiens, 2007), vertebrates generally (Grenyer et al., 2006), and epifaunal invertebrates (Witman et al., 2004). Global level datasets supporting richness and endemism analyses now exist and contain information on more than 30,000 species of vertebrates, including birds, mammals, reptiles, and amphibians (Kier et al., 2005).

However, plants are key structural elements of terrestrial ecosystems and are the basis of all terrestrial food webs. They are of great relevance in understanding global distribution of diversity and play a central role as an indicator group (Kreft & Jetz, 2007). Hence, plant richness patterns have been used extensively for global-scale conservation prioritizing (Myers et al., 2000; Mittermeier et al., 2005). Furthermore, detailed information about spatial patterns of phytodiversity is a central prerequisite to fulfill targets set by the Convention on Biological Diversity (CBD) and the Global Strategy on Plant Conservation (GSPC), which include protecting 50% of the most important centers of plant diversity and to conserve 60% of the world's most threatened species *in situ* by the year 2010 (Barthlott et al., 2005).

To date, papers investigating various aspects of global plant species richness patterns and diversity and global species numbers have almost exclusively focused on vascular plants. Yet, other groups such as liverworts are of critical

biological, ecological, and phylogenetic significance. A growing body of evidence identifies liverworts as the earliest diverging lineage of embryophytes. Their sister relationship to all other land plants puts liverworts in a pivotal position in our understanding early land plant evolution (e.g., Mishler et al., 1994; Wellman et al., 2003; Qiu et al., 1998, 2007). Liverworts are an important component of the vegetation in many regions of the world, constituting a major part of the biodiversity in moist forest, wetlands, mountain, and tundra ecosystems (Hallingbäck & Hodgetts, 2000). Liverworts and mosses offer microhabitats that are critical to the survival of a tremendous diversity of organisms such as single-celled eukaryotes, protozoa, and numerous groups of invertebrates (Gerson, 1982). Their structural contribution to levels of diversity might be as significant as that of vascular plants, albeit at a smaller scale. Liverworts, in concert with mosses and hornworts, play a significant role in the global carbon budget (O'Neill, 2000) and CO₂ exchange (De Lucia et al., 2003), plant succession (Cremer & Mount, 1965), net production and phytomass (Frahm, 1990), nutrient cycling (Coxson, 1992), and water retention (Pócs, 1980; Gradstein et al., 2001). These plants also are important environmental and ecological indicators (Rao, 1982; Pitcairn et al., 1995; Gradstein et al., 2001; Giordano et al., 2004) and have been used as indicators of past climate change, to validate climate models, and are potential indicators of global warming (Gignac, 2001).

Recently, we created the first comprehensive global database uniting liverwort nomenclature, taxonomy, and geography; the preliminary dataset includes the distribution of liverwort species across almost 400 geopolitical units based on some 60,000 records from over 600 publications (von Konrat et al., *in press*). We contended that this database has much to offer also to the broader biological community, not only through aiding our understanding of liverwort diversity.

Moreover, good quality data on liverwort diversity has a multitude of applications, such as powerfully informing biogeographic and conservation research as well as identifying data-deficient regions.

Here we have used this database to 1) provide global maps for liverwort species, genera, and family richness, 2) investigate the relationship between taxon richness at the species level and higher taxonomic levels, and 3) present a comparison of centers of species richness between liverworts and vascular plants. The global maps, presenting political units, summarize the total number of taxa at the rank of species, genus, and family. By examining the relationship between species richness and higher level taxonomy we test Gaston and Williams's (1993) supposition that patterns of species richness can be studied from taxonomic levels higher than species. Finally, the comparison of centers of species richness between liverworts and vascular plants has two immediate implications. First, patterns of vascular plant species richness have been used, as mentioned, for priority setting of global scale conservation networks. Secondly, vascular plant species diversity has been used as a predictor of bryophyte species diversity in some forest systems (Chiarucci et al., 2007).

We close with the conclusion that increased knowledge of liverwort species distribution has far reaching implications and applications. There is an urgent and sustained need to develop such baseline knowledge, from which our understanding of the variability of plant species richness at a global scale ultimately flows.

Methods

Quality of Underlying Data

A brief discussion of the quality of the underlying dataset used here to produce the global maps and statistical analysis is provided by von Konrat et al. (in press). In brief, names obtained primarily from geopolitical checklists were cross-referenced against taxonomic revisions, monographs, and authoritative indices (e.g., Crosby & Engel, 2006) for synonyms and verification of distribution. A very brief assessment on data availability and information needs specifically for liverworts was provided by von Konrat et al. (in press) Our

dataset, based on over 600 publications, currently includes some 22,500 published liverwort names ("accepted" taxa and synonyms), 60,000 observations (defined as one taxon recorded from one geopolitical unit), and almost 500 geopolitical units (von Konrat et al., in press). The maps and statistical analysis are based on what we assume to be the approximately 6,500 currently "accepted" binomials to date. All names that could not be reconciled through our cross-referencing, as well as infraspecific taxa, were excluded from the analysis.

Mapping and Statistics

MAPPING—The global distribution maps of species, genera, and family richness were produced using the inventory-based mapping approach, which is explained by Mutke and Barthlott (2005). They reflect numbers per geopolitical unit without standardization for area. The comparison of the top 20% of the centers of species richness between liverworts and vascular plants is defined as >110 spp./10,000 km² for liverworts, and $>3,000$ spp./10,000 km² for vascular plants (Barthlott et al., 2005). Species richness in this comparison refers to an area of 10,000 km² standardized by the species–area model of Arrhenius (1920, 1921). We used the value 0.25 for the parameter z that determines the slope of the species–area relationship in this model. This value has been widely used (e.g., Rosenzweig, 1995) and is within the range of z -values found in other large-scale analyses of plant diversity patterns (Kier et al., 2005; Qian, 2007). This standard area offers a sufficient spatial resolution and is regarded as suitable for large-scale conservation approaches (Mutke & Barthlott, 2005).

STATISTICS—We explored the relationship between species richness and genus richness, and species richness and family richness through linear regression analysis, because we were primarily interested in the nature of the relationship between these pairs of variables. We established that the relationship between the variables was significant with an ANOVA, and used the Residual mean squares from the ANOVA as the primary basis for our comparison of the fit of our data to linear and various simple polynomial models. Analysis and graphics were produced and performed using SPSS 15.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results and Discussion

Described Species Over Time

Figure 1 depicts the number of novel liverwort species, excluding new combinations that have been described over the last 250 years. The first major peak corresponds to the works of several early 19th century botanists, including *Synopsis Hepaticarum* by Gottsche, Lindenberg, and Nees (1844–1847). The three decades leading into, but prior to the highest peak, between 1860 and 1890, corresponds to the publications by a number of prominent bryologists including W. Mitten, J. D. Hooker, T. Taylor, and V. Schiffner. The second and highest peak of almost 1,200 names, in the early 1900s corresponds largely to the plethora of taxa described by Stephani (1898–1924) in his monumental work *Species Hepaticarum*. The periods of highest rates of new species described in the 1830s and around 1900 are the same for seed plants (Mutke & Barthlott, 2005). The third peak over the four decades between 1950 and 1980 can be attributed mainly to the works of R. M. Schuster, H. Inoue, and S. Hattori. The decline in newly described species since 1970 does not necessarily wholly translate to the supposition that taxonomists are closer to discovering all known species.

The almost 200 novel liverwort species that have been described in less than the past six years alone still represent a significant number, considering the relatively few liverwort taxonomists and monographers. Moreover, bryological exploration has been very uneven in many parts of the world; for example, many areas of the Neotropics

still remain without a single bryophyte record (Gradstein et al., 2001). Paradoxically, scores of new species are still being discovered and described in relatively well-studied areas such as New Zealand; e.g., 12 new taxa in *Lepidozia* (Engel & Schuster, 2001). Recent attention to cryptic speciation in bryophytes is also revealing novel liverwort species; e.g., Szweykowski et al. (2005). The combination of collecting in yet-to-be explored areas, the continued discovery of species in well-studied regions, and an increased understanding of the biology of liverworts (including cryptic speciation), will lead to a significant number of newly discovered species into the foreseeable future. The corollary of this, coupled with increased monographic and revisional work, will be the increased discovery and the unraveling of synonymy.

Despite the fact that discovery and description of liverworts has continued for over 250 years, there has been no central source working toward a synthesis of nomenclature, taxonomy, and global distributional data until recently. This has been a major impediment for the study and analysis of species richness, distribution patterns, and conservation at a regional and global scale. There remains no reliable quantitative data with which the global number of liverwort species can be estimated objectively. Nevertheless, reliable figures of the global number of extant species are in great demand and have been seen as a fundamental descriptor of life on Earth (Gaston & Hudson, 1994) as well as important to assist conservation and decision-making (Govaerts, 2001). With support from the bryological community, we are

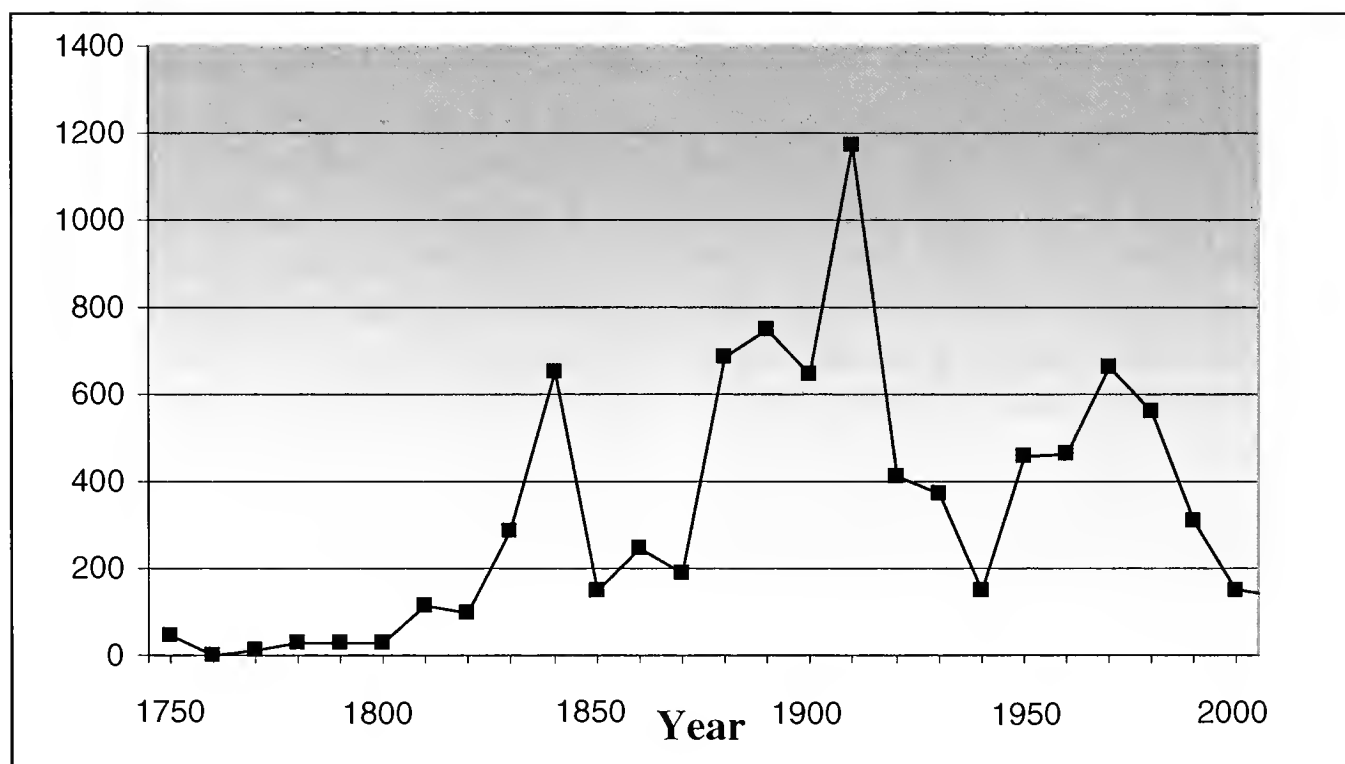


FIG. 1. The number of novel liverwort species described over 250 years from 1750 to the present (numbers exclude new combinations and are based on our unpublished dataset).

now working toward centralizing this information; e.g., Söderström et al. (this volume) and von Konrat et al. (in press). Below, we apply that dataset to providing a summary of global diversity, including species, genera, and family numbers, on a global scale, the relationship of liverwort species richness to higher taxonomy, and a comparison of centers of species richness between liverworts and vascular plants.

Numbers of Species, Diversity, and Distribution

Species richness is the simplest way to describe community and regional diversity (Magurran, 1988), and this variable—number of species—forms the basis of many ecological models of community structure (MacArthur & Wilson, 1967; Connell, 1978; Stevens, 1989). Mutke and Barthlott (2005) produced a world map of species numbers per country/state for mosses and stated that the documentation of patterns of bryophyte diversity is still very incomplete. Pócs (1996) provided an evaluation of 1,000 epiphyllous liverwort species on a global scale, assessing their diversity, degree of threat, and conservation. Recently, von Konrat et al. (in press) produced the first-ever preliminary global map of species richness of liverworts, presenting species density values for standard area sizes of 10,000 km² throughout the world. Here, we present the number of liverwort species, genera, and families per geopolitical unit (Figs. 2–4) offering an easy and quick guide to identifying richness across the three taxonomic ranks worldwide based on our preliminary global dataset. It must be stressed that these numbers only offer a guide to liverwort diversity and the dataset is in a constant state of flux as 1) new data comes to hand, 2) increased monographic and revision work takes place, and 3) data are acquired from undercollected regions of the world.

Areas representing the highest class of between 501–777 liverwort species numbers include 601 documented binomials for New Zealand (Engel & Glenny, 2008), 615 for Japan (Furuki & Mizutani, 2004), 561 for Costa Rica (Dauphin, 2005), 514 for the Philippines (Tan & Engel, 1986), 608 for the island of Borneo (Menzel, 1988), 752 for Colombia (Bernal et al., 2007), and 606 for continental Ecuador (León-Yáñez et al., 2006). The latter three areas (Borneo, Colombia, and Ecuador) do not coincide with the global maxima of liverwort species after being standardized for

area as presented by von Konrat et al. (in press). In some regions such as India, the data have been aggregated at the country level because there are no reliable data at a smaller scale. Hence, India, too, falls into the highest class. However, the majority of the species, over 500, occur in the north of India (e.g., Kashmir and the Himalayas), whereas the remaining regions of India (e.g., Punjab, Rajasthan, Gujarat, central India, the Gangetic Plain, and south India) have less than 250 species. The unrealistically low class of 16–50 documented binomials in areas such as Gabon, Congo, and the Malayan Peninsula where there are over 3,000 vascular plant species per 10,000 km² (Mutke & Barthlott 2005), is a direct reflection of our dataset that illustrates a lack of adequate information on liverworts from those regions. Equally, Figure 2 illustrates areas without or with very few species, the class representing 1–15, including large parts of the Sahara and the Kalahari Desert, as well as the arid and semiarid regions of central and south Australia; this almost certainly reflects genuine lack of diversity. These minima coincide with a lack of either available ambient energy or humidity, which limits plant growth and corresponds to the low number of vascular plants (Barthlott et al., 2005).

Interestingly, the areas with the highest number of species do not necessarily correspond precisely to those with the highest number of genera or families (Figs. 3, 4). For instance, New Zealand and Japan are represented by the highest classes of 501–777, 128–151, and 46–49 for species, genus, and family, respectively. Colombia, by contrast, is represented in the highest class for species and genus, but only the third highest class of 36–40 for family. Similarly, Ecuador, which also falls into the highest class for species, falls in the second highest class for genus, and the third highest class for family. These slight differences can be attributed to the relatively large number of endemic genera or monotypic genera that occur in areas such as New Zealand. On the other hand, areas such as Colombia, which lie in the tropics, are represented by a disproportionate number of members representing Lejeuneaceae. Lejeuneaceae is the largest family of liverworts with an extant diversity of approximately 1,000 species in some 90 genera (Gradstein, et al., 2003), and in some areas of tropical lowland forests, Lejeuneaceae can make up 70% of all liverwort species (Cornelissen & Ter Steege, 1989; Zartman, 2003; Gradstein, 2006). The section below explores the relationship between species richness and higher level taxonomy.

Despite the constraints and challenges in obtaining high quality data to quantify global liverwort diversity, we now have a dataset that can be applied to investigate liverwort distribution patterns. Future global mapping of liverwort species richness needs to be explored by ecoregion rather than by political units in a fashion similar to what Kier et al. (2005) have produced for vascular plants. This will lead to more biologically and ecologically meaningful interpretation of liverwort diversity patterns. Lack of a totally resolved taxonomy with all “accepted” species named and their range defined, although hampering, should not preclude us from making such analyses. As in any other field of science, taxonomy will always be in flux, aptly quoted by May (1990) “taxonomy is the destiny” because new data will always come to hand. Yet, for future global mapping and distribution analyses, it will be essential to consider and distinguish between those species that remain poorly documented, and thus too poorly known for analyses, and those species that are widely accepted as accurate descriptors of biological diversity.

Species Richness and Higher-Level Taxonomy

Species richness is a fundamental measure of biodiversity, and declining species richness in many regions of the world is a major ecological, economical, and cultural problem (Bergamini et al., 2005). The practical challenges in describing and enumerating species richness, including the problem of the enormous amount of resources (e.g., time, money, taxonomists) have urged conservation biologists to identify reliable surrogate measures for explaining patterns in biodiversity (Balmford et al., 1996; Heino & Soininen, 2007). These surrogacy methods include environmental characteristics, indicator taxon groups and individual indicator species, and use of higher taxonomic levels (Gaston & Blackburn, 1995; Faith & Walker, 1996; Williams et al., 1997; McGeogh, 1998; Ward et al., 1999; Heino et al., 2003; Fleishman et al., 2005; Wolters et al., 2006). Recently, Moreno et al. (2007) provided a brief review of these rapid alternative routes for appraising species diversity.

Gaston & Williams (1993) suggested that patterns of species richness could be studied from higher taxonomic levels. Their preliminary analyses indicated that predictions might be quite reasonable, cost effectiveness might be high, and

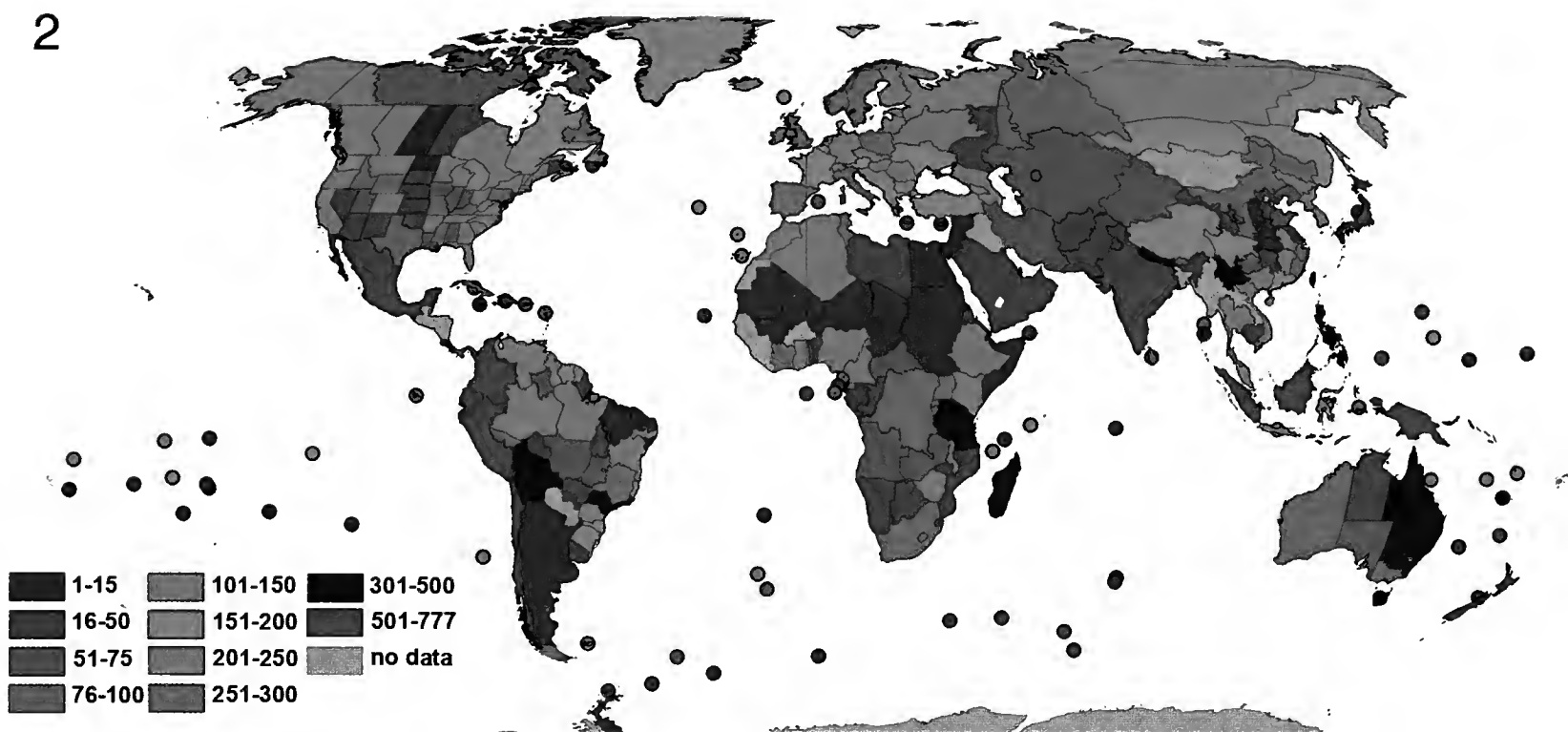
that substantial bodies of data already existed. Another crucial advantage is the retention of broad biological information that allows the understanding of distribution patterns (Eggleton et al., 1994; Williams et al., 1994; Gaston & Blackburn, 1995) and more efficiency in the definition of conservation priority areas (Williams, 1993; Williams et al., 1994; Vanderklift et al., 1998; Balmford et al., 2000). Numbers of higher taxa can also provide some measure of another dimension of diversity, the dissimilarity or disparity between organisms (Williams, 1993). Higher taxa have also proven to be useful in environmental and impact studies (Beattie & Oliver, 1994; Somerfield & Clarke, 1995).

This approach has since been applied to a variety of biological groups, with studies showing significant positive correlations between higher taxon richness and species richness (e.g., Gaston & Williams, 1993; Williams & Gaston, 1994; Roy et al., 1996; Balmford et al., 1996, 2000; Cardoso et al., 2004; Villaseñor et al., 2005). Diversity at higher taxonomic levels has also long been regarded as a good surrogate for diversity at the species level by palaeontologists (Sepkoski, 1992). On the other hand, some studies have found that higher taxon analyses are weak predictors of species richness (Prance, 1994; Andersen, 1995; Fjeldsa, 2000), suggesting that this is not necessarily an infallible remedy when it comes to estimating the patterns of species richness (Grelle, 2002).

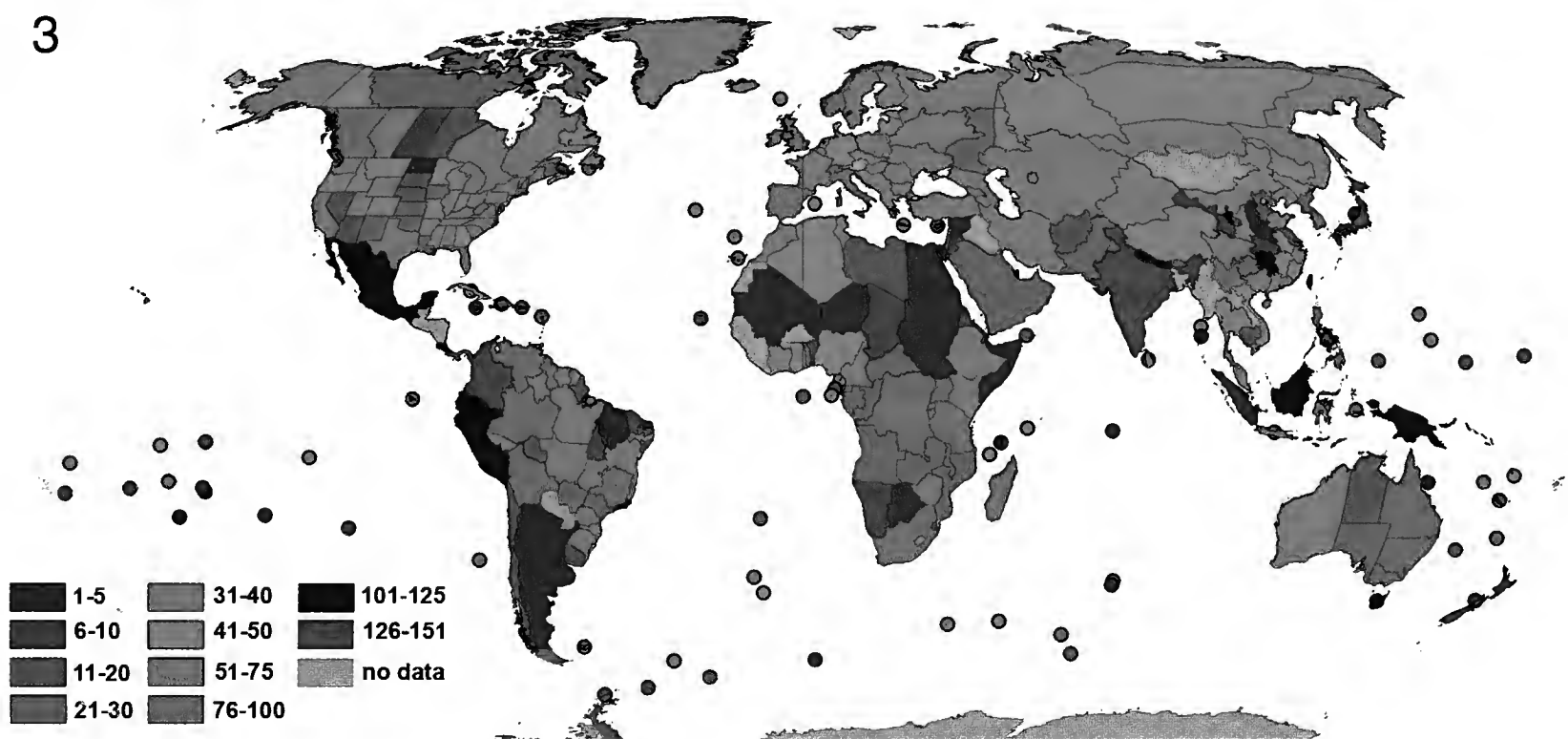
We here examine the utility of using higher taxa as potential surrogates for liverwort species richness by testing the relationship between species richness and the numbers of higher taxa, i.e., genera and families.

SPECIES VS GENERA—Box plots for the raw number of species and number of genera were both positively skewed (Appendix I). A scatterplot of number of species against number of genera (Fig. 5) and a plot of residuals against predicted number of species (not shown) from a linear regression analysis both suggested a nonlinear relationship between these two variables. The boxplots of species and genera were both strongly positively skewed. The nature of the species vs. genera relationship appears quadratic. For simple polynomial models of the form $y = a + x^2$, by defining $w = x^2$, we get a simple linear model, $y = a + bw$, with which we can estimate x^2 using traditional linear regression procedures. The boxplots for species were only slightly positively skewed after the data was square-root

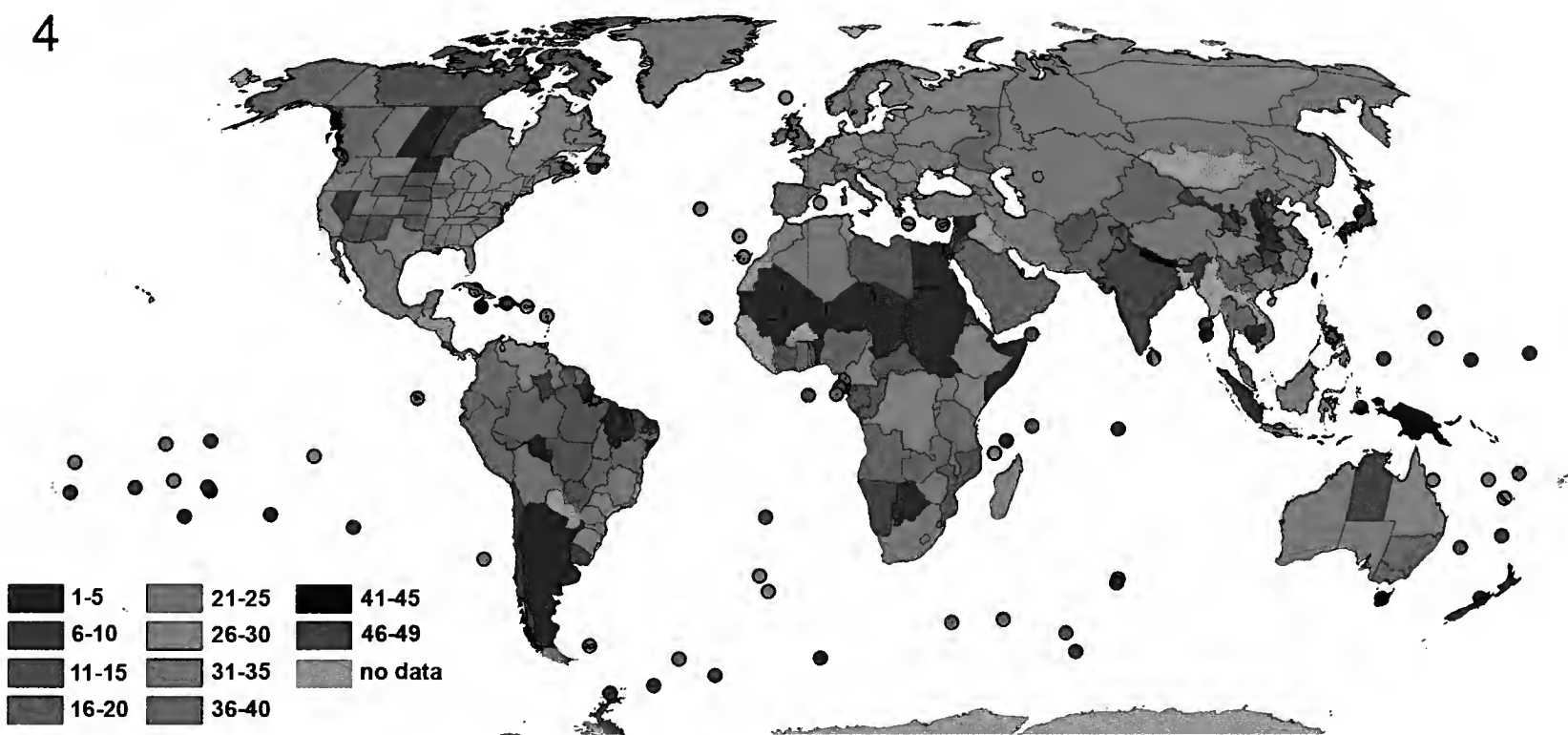
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3



4



FIGS. 2–4. Maps of the numbers of liverworts per political unit: 2, Species numbers; 3, Genus numbers; 4, Family numbers.

transformed (Appendix I). A plot of residuals against predicted number of species from a linear relationship substituting w for x shows no evidence of a nonlinear relationship. Following transformation, plots of residuals against genera showed a cloud-like distribution, suggesting homogeneity of variances (not shown).

The t -test and the ANOVA F -test cause us to reject the null hypothesis that the slope of both linear and quadratic regressions equals zero (Appendices 2 & 3). The r^2 indicates that we can explain about 88% of the total variation in species number with the linear relationship, but about 95% with the quadratic relationship. Pearson's correlation coefficient is also higher for the quadratic model (0.974 vs. 0.940), indicating that this relationship is stronger than the linear. The Residual Mean Squares are less for the quadratic (882.16 vs. 1994.74), which means that the points all lie closer to the line than in the linear. This indicates again that the quadratic is a better fit, and this can be seen visually (Fig. 5).

SPECIES VS. FAMILY—Quadratic models again provide a better explanation of the data by the same metrics as described above (Appendices 4 & 5). The scatterplot of number of species against number of families also exhibits a nonlinear relationship (Fig. 6). The r^2 indicates that we can explain about 59% of the total variation in species number with the linear regression, but about 69% with the quadratic equation. Pearson's correlation coefficient is also higher for the quadratic (0.829 vs. 0.770), indicating that this relationship is stronger than the linear. Yet, the fact that the Residual Mean Square is much higher for this

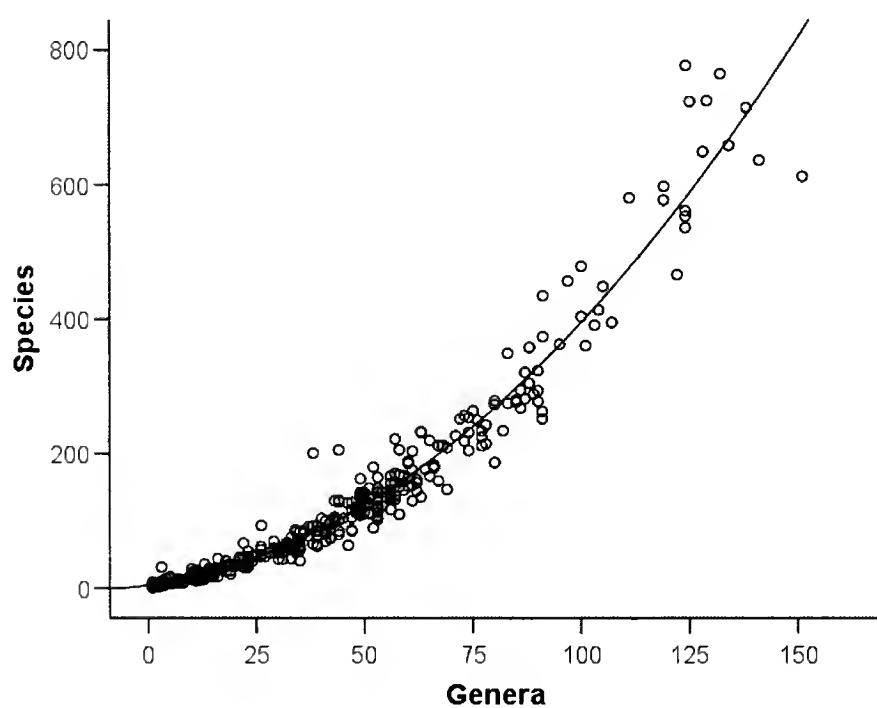


FIG. 5. Relation of generic richness to species richness.

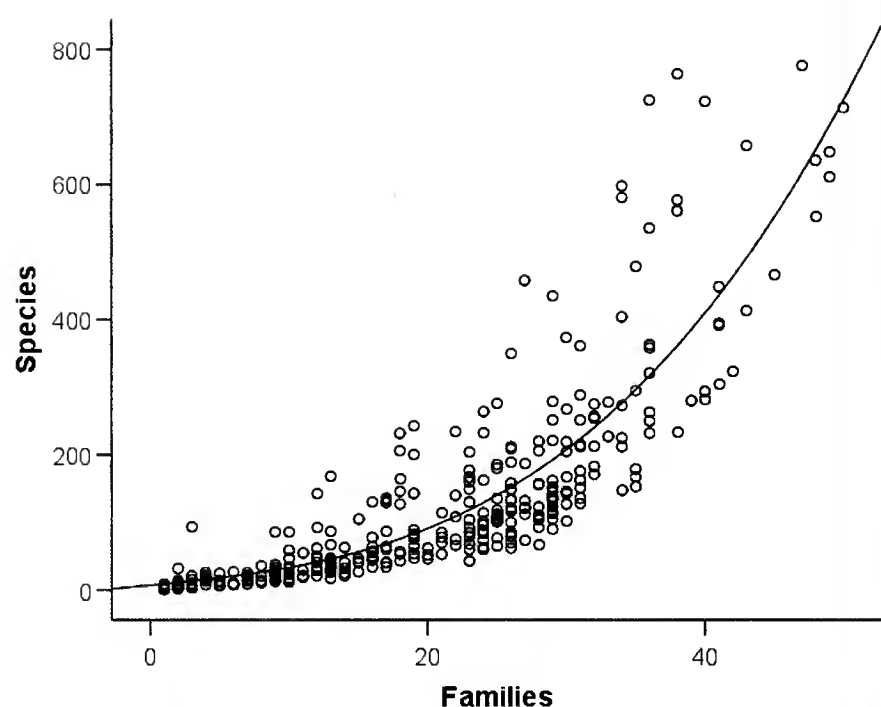


FIG. 6. Relation of familial richness to species richness.

model means that the relationship is not so tight as between species and genera. The scatter of points around the regression line is considerably positively skewed in this relationship, and this is reflected in a plot of residuals against predicted number of species.

HIGHER-TAXON ANALYSIS AS A SURROGATE FOR SPECIES RICHNESS—Analyses based on our dataset showed that generic richness was slightly more related to species richness than that of the families. Quadratic models also appear to explain a greater variation of species number than linear models. In summary, it is suggested that the higher-taxon approach at the generic level might be a useful surrogate of species richness. The higher-taxon α -diversity, especially at the generic level, has now been shown to be a useful surrogate across a wide biological spectrum. For mammals (Grelle, 2002), ants (Andersen et al., 2004), spiders (Cardoso et al., 2004), macrofungi (Balmford et al., 2000), macrolichens (Bergamini et al., 2005), and plants (Balmford et al., 1996; Villaseñor et al., 2005), the higher-level taxon surrogate approach at the generic level is useful, but the relationships between number of species and families or orders are weaker.

This dataset has the potential to be explored in more detail and the reliability tested depending on habitat, biogeography, and sampling effort. The data can be partitioned and geographical variability at a regional scale can be explored. Partitioning of the data sets by taxon and geography also will aid in identifying the potential problem of para- and polyphyletic taxa as well as assessing the impact that genera and families are not necessarily comparable units because of

their different life histories. We can also begin to explore such questions as: Can total liverwort species richness be predicted by the richness of liverwort genera alone or particular liverwort genera? and Do liverwort genera alone reflect compositional shifts in liverwort communities? Diversity patterns of higher taxa might also provide valuable insight into evolutionary, historical, and biogeographical influences on contemporary diversity (Ricklefs, 1987).

Comparison of Liverwort and Vascular Plant Species Richness Patterns

Diversity patterns of vascular plants have almost always been included in analyses for priority setting of global scale conservation networks (e.g., Myers et al., 2000; Olson & Dinerstein, 2002; Mittermeier et al., 2005). We therefore evaluated the relationship between the top 20% centers of species richness for liverworts and vascular plants (Fig. 7), which is defined as >110 sp./10,000 km² for liverworts, and $>3,000$ spp./10,000 km² for vascular plants (Barthlott et al., 2005); the top 10% is also illustrated for liverworts which equates to >251 sp./10,000 km². Many centers with high liverwort species richness, e.g., New Zealand and Japan, are outside the top 20% centers of vascular plant species richness.

However, because of the extraordinary high rate of vascular plant endemism coupled with the degree of habitat threat, these regions have been designated biodiversity hotspots (Myers et al., 2000; Olson & Dinerstein, 2002; Mittermeier et al., 2005). Figure 7 illustrates other areas with high liverwort species richness such as Costa Rica, the Himalayas, and the island of Borneo which coincide with the top 20% centers of vascular plant species richness. These same areas are also part of designated global biodiversity hotspots, i.e., Mesoamerica, Himalaya, and Sundaland hotspots, respectively (Mittermeier et al., 2005).

Conversely, it is also apparent that there are many regions that exhibit significantly high levels of liverwort species richness but do not coincide with any of the top 20% centers of vascular plant species richness. These areas include southern Chile, the British Isles, Taiwan, and Tasmania and Queensland of Australia. Nor do any of these areas coincide with any existing biodiversity hotspot region as defined by Mittermeier et al. (2005). Considering that bryophytes are a conspicuous and dominant feature in many ecosystems throughout these regions, further analysis is warranted. In summary, a potential weakness of approaches that are heavily weighted towards vascular plant species richness and endemism for identification of global biodiversity hotspots is that they neglect very important centers of

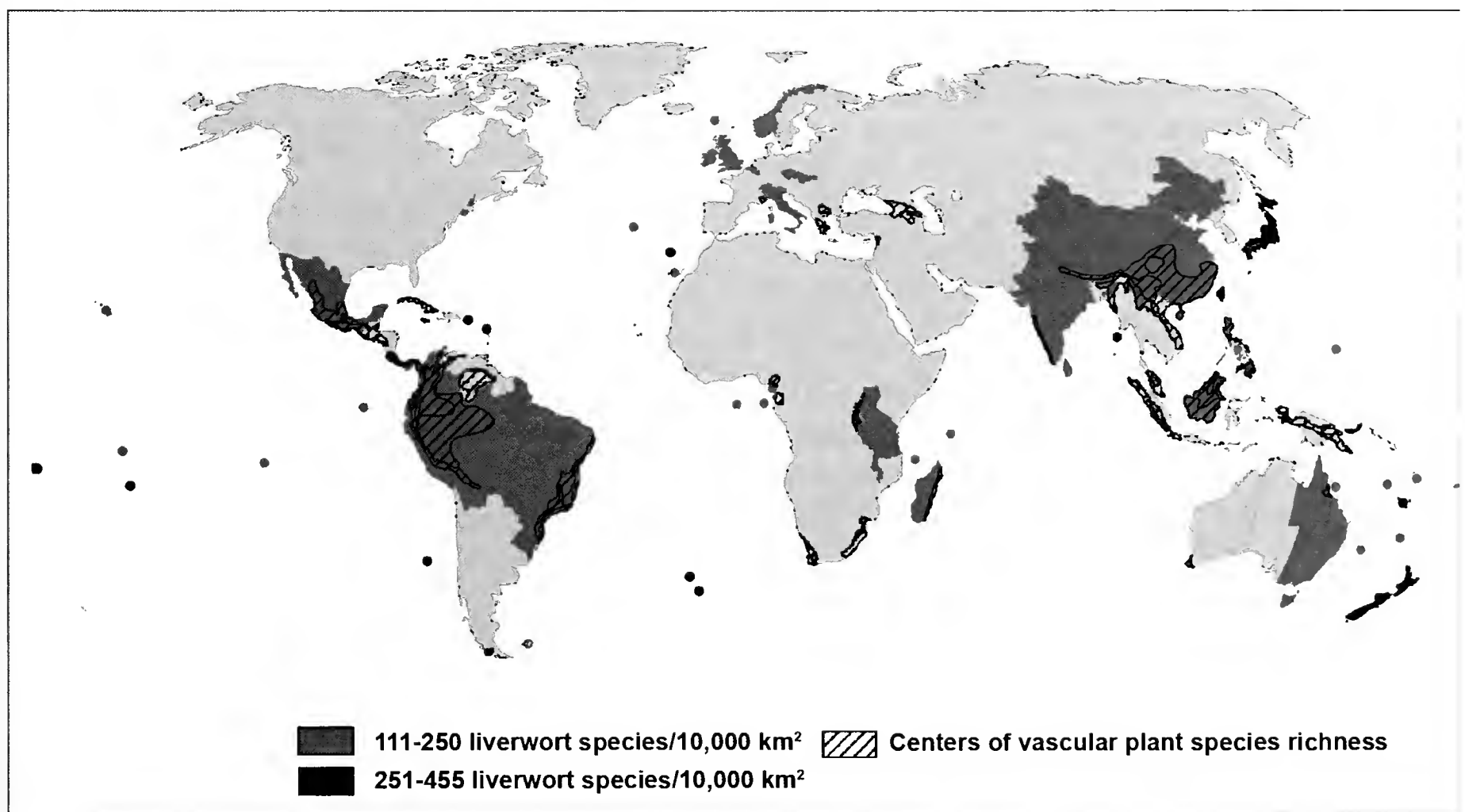


FIG. 7. Map of centers of high species richness of liverworts and vascular plants.

liverwort diversity, which lie outside existing biodiversity hotspots.

Conclusion

Liverworts, together with mosses and hornworts, are of great ecological and biological significance worldwide. To date, papers investigating various global plant species richness and diversity patterns have almost exclusively focused on vascular plants. The bryological community is now working toward developing a high quality dataset quantifying global liverwort diversity. Many promising areas of research are now possible with this new dataset and can contribute toward understanding the forces that shape spatial and temporal variation in liverwort diversity as well as for conserving and managing liverwort biodiversity. The global maps produced here provide a quick overview of richness on a global scale at different levels of taxonomic hierarchy. Future global mapping efforts should include liverwort species richness by ecoregions and investigations of the environmental and potential historical determinants of liverwort richness. Endemism should also be assessed in future mapping efforts.

Ideally, the study of patterns of biodiversity should be carried out using species-based datasets. However, in some instances, identification of reliable surrogate measures for explaining patterns in biodiversity might be warranted. The analyses performed here showed that higher taxon analysis, especially at the generic level, has potential to be used as a reasonable surrogate for species richness. It is now important to determine the degree to which higher taxa perform as species-level biodiversity surrogates in regions differing in species diversity and in other taxonomic groups.

Greater consideration of liverworts can now be made in evaluating global networks of protected areas. This is underscored by the importance and abundance of liverworts in many habitats throughout the world and the fact that some centers of species richness lay outside many centers of vascular plant species richness, which are often used to create these networks. In future studies, it would be interesting to investigate the underlying factors, e.g., geological, climatological, or historical, that might explain the lack of total overlap between centers of liverwort diversity with those of vascular plants and different animal groups.

Many applications of this dataset are now possible and can contribute towards the creation of a comprehensive global biodiversity strategy for the terrestrial realm where already large datasets occur for vascular plants, mammals, birds, and amphibians.

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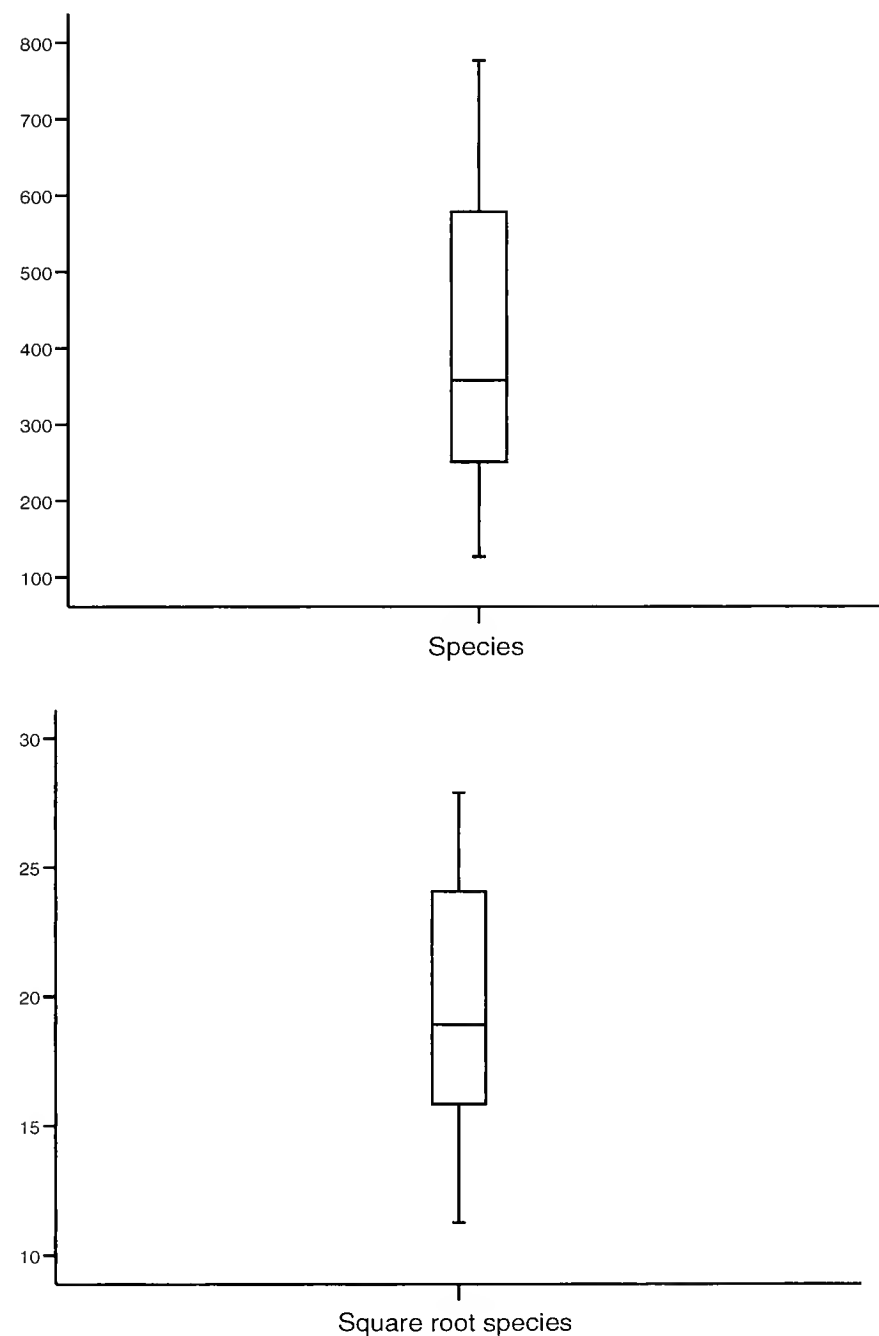
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ZARTMAN, C. E. 2003. Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. *Ecology*, **84**: 948–954.

Appendix I. Boxplots for transformed variables.

Species, skew = 0.375 (mild positive skew).
Square root species, skew = 0.077 (where 0 is no skew).



Appendix II. Linear regression statistics: species vs. genera.

	Coefficient	Standard error	Standardized coefficient	<i>t</i>	<i>P</i>
Intercept	-50.90	4.4		-11.57	<0.001
Slope	4.08	0.08	0.940	48.38	<0.001
Correlation coefficient (<i>r</i>) = 0.940, <i>r</i> ² = 0.883					
Source	df	MS	F	<i>P</i>	
Regression	1	4668941.7	2340.6	<0.001	
Residual	311	1994.7			

Appendix III. Quadratic regression statistics: species vs. genera.

	Coefficient	Standard error	Standardized coefficient	<i>t</i>	<i>P</i>
Intercept	1.871	3.955		0.473	0.637
Slope	0.027	0.01	0.732	19.830	<0.001
Correlation coefficient (<i>r</i>) = 0.974, <i>r</i> ² = 0.948					
Source	df	MS	F	<i>P</i>	
Regression	2	2507917.61	2842.92	<0.001	
Residual	310	882.16			

Appendix IV. Linear regression statistics: species vs. family.

	Coefficient	Standard error	Standardized coefficient	<i>t</i>	<i>P</i>
Intercept	-59.571	9.800		-6.079	<0.001
Slope	9.200	0.432	0.770	21.285	<0.001
Correlation coefficient (<i>r</i>) = 0.770, <i>r</i> ² = 0.593					
Source	df	MS	F	<i>P</i>	
Regression	1	3136332.508	453.048	<0.001	
Residual	311	6922.740			

Appendix V. Quadratic regression statistics: species vs. family.

	Coefficient	Standard error	Standardized coefficient	<i>t</i>	<i>P</i>
Intercept	26.688	12.376		2.157	0.032
Slope	0.312	0.032	1.082	9.692	<0.001
Correlation coefficient (<i>r</i>) = 0.829, <i>r</i> ² = .688					
Source	df	MS	F	<i>P</i>	
Regression	2	1818502.050	341.182	<0.001	
Residual	310	5330.002			

FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Five: Liverworts—Globally and Locally

Chapter Ten: Early Land Plants Today: Liverwort Checklist of Checklists

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Abstract

The significance and importance of checklists is briefly discussed. A comprehensive current checklist of liverwort checklists is provided with the starting date of 1900. In order to increase the value of this list, the checklists have been categorized according to whether the publications are specimen-based, record original citations, or list the extent of the territory covered. Although there are checklists for many territories throughout the world, there remain, alarmingly, substantial portions of the globe that either lack checklists entirely or have checklists that are woefully out of date.

Introduction

Target 1 of the Global Strategy for Plant Conservation (GSPC), adopted as part of the

Convention on Biological Diversity (CBD), states that a working list of all known plant species is a fundamental requirement to underpin plant conservation actions, and sets a target date of

2010 (Lughadha, 2004). As early as 1881 Charles Darwin expressed a wish to have a catalogue of all known plants (Crane, 2004). However, over 125 year later, this wish is not yet fulfilled! Without a working checklist, many of the other objectives in the GSPC cannot be met and botanists around the world cannot communicate about plants on a global basis (Crane, 2004). A preliminary global checklist for mosses has been completed (Crosby et al., 1999) but there is nothing near that for liverworts, although attempts to produce one are in progress (von Konrat et al., 2008).

Checklists have two main objectives. First, they provide a standard list of which taxa exist in a defined territory or area. Standardization is critical because different authors use different taxonomy and nomenclature, making comparison otherwise difficult (see e.g., Isaac, 2004). Checklists are thus tools for harmonizing nomenclature and taxonomy, a clear advantage for communication and comparative study. Such lists should then also include an extensive synonymy list to explain the concepts used.

Secondly, checklists are summaries of distributions. Information on distribution and reports of new records or range extensions are also vastly scattered in the literature. Many of these reports are looked upon as of minor and local interest and thus are published in local journals where they are hidden from the broader scientific community and public. Checklists are therefore powerful and important tools that can integrate the almost overwhelmingly scattered information concerning taxonomy, systematics, nomenclature, distribution, and even frequency. Analysis of biogeographical patterns, e.g., distribution patterns (Söderström & Senecca, 2006) or rarity patterns (Söderström et al., 2007a), will be more accurate if all information is readily available as in a checklist. The smaller the geographical areas used in the checklist, the more precisely the distribution that can be mapped. Checklists also are required in order to establish baselines for the future and to be able to monitor change in the flora, including possible extinctions.

In Europe, good checklists that are regularly updated have been published for a long time. However, lists differ in their construction. For example, Grolle and Long (2000) only listed the names of the species occurring in Europe and Macaronesia, thus fulfilled mainly the first of the abovementioned objectives of a checklist. Söderström et al. (2002) used the same taxonomy but indicated each country species were reported

from, i.e. supplemented with the second objective.

Checklists have the built-in problem that they are out of date as soon as they are published because new data accumulates rapidly. For this reason, updates must be published regularly to maintain the utility of the checklist over a longer time, a task more easily done with checklists than with floras that can take years to produce. As an example, Söderström et al. (2007b) updated Söderström et al. (2002) with new taxonomic, nomenclatural, distribution, and Red Listing information for 437 species of the European liverwort and hornwort flora between 2002 and 2007. Yet, checklists can provide a very efficient and effective means to quickly summarize information, in contrast to floras that can take years and often decades to produce. Furthermore, although one of the many objectives of a monograph or flora is the key problem of how to detect synonymy, this can be more quickly accomplished, at least to a first approximation, through efforts to develop synonymized checklists (Crane, 2004).

The use of web technology will in time offer the most effective mechanism to provide the most up-to-date information, in a similar manner to the increasing number of floras which have online versions that easily can be modified and updated.

One problem often seen is that species erroneously reported from an area continue to be reported based on the rejected source. A good checklist should therefore clearly state that such errors have been considered but rejected, even if this is only a repetition of an earlier rejection.

Types of Checklists

There are many different kinds of checklists based on the territory and taxa covered. The area that is covered can range from a continent (e.g., Europe; Grolle & Long, 2000) to a small park (e.g., Hubbard Brook Experimental Forest; Cleavitt & Fahey, 1996). Some lists covering large areas provide reports by subdivisions; for example, the Mediterranean checklist by Ros et al. (2007) that indicates occurrences in the individual countries, or the checklist of Bolivia by Gradstein et al. (2003) which indicate reports from individual provinces. Species lists for the subdivisions can be extracted from lists such as these.

The taxa covered by a list can vary from a single genus (e.g., *Lejeunea* in Latin America; Reiner-Drehwald, 1999) upward to all liverwort taxa. Checklists also vary in the way they are compiled and presented. The simplest checklist is a compilation of literature reports where the sources of individual records are cited (e.g., Yano, 1984 for Brazil; Tan & Engel, 1986 for the Philippines) or where the sources of individual records are not cited (e.g., Söderström et al., 2002 for Europe). More complex are those checklists based on verified specimens (cf. Koponen et al., 1998). In such lists, specimens can be cited (e.g., Grolle & Piippo, 1984) or not cited, the latter often citing localities instead (e.g., Popova & Zolotov, 1998).

One problem sometimes encountered in checklists is to know which taxon is meant with a particular name. An example of a classical problem is that the name *Harpalejeunea ovata* can be considered a synonym of *Douinia ovata* [*H. ovata* (Dicks.) Schiffn.] or *H. molleri* [*H. ovata* (Hook.) Steph.], depending on the authorities. Thus, to avoid such problems, author citations should be fully indicated. A more difficult problem is with names such as *Calypogeia trichomanis*, which have been misapplied to more than one taxon. Although the type specimen of *C. trichomanis* belongs to *C. fissa*, the former name has been used for several taxa in the past, most frequently (at least in Europe) for *C. azurea*. Here one can only guess what is meant based on the other names of the genus in the list.

Koponen et al. (1998) gave four principles for compiling a good checklist. **Principle 1:** “*The basic principle of all checklists is that they should be based on herbarium specimens which can be traced and the identity of which can be checked, when or if necessary.*” A checklist only based on literature can indirectly fulfill this criterion because specimens might be cited in the earlier publications. **Principle 2.** “*Floras lacking documentation should be used very critically as basis of checklists.*” If no specimen is cited, it is difficult to know if the description is based on material from within the area covered by the flora, or from an area where it is more common. In the latter case it might turn out that the local taxon is not what is described in the flora. **Principle 3.** “*Popularizing books and plant sociological papers lacking documentation should be omitted or used very critically as basis of checklists. Records in unpublished manuscripts and data files not generally available should not be used as bases of checklists.*” One of the main aims of a checklist is to make information more accessible

to more people. An explanation of the content of these sources and an indication of if/where specimens might be deposited also are highly desirable. Doubtful information should be identified and commented on, and perhaps rejected until positively confirmed. **Principle 4.** “*The information in the checklists should be given in an easily available form.*” This cannot be stressed enough!

A Current Checklist of Liverwort Checklists

There have been two earlier compilations of liverwort checklists. Lane (1978) listed the bryophyte floras of the world and Greene and Harrington (1989) made an extensive compilation not only of checklists but included also extensive species lists of other kinds. The aim here is to list checklists that might form the basis for a global checklist that includes data on species distribution. In order to restrict the list here (there exist a lot of published checklists), only checklists that cover a “reasonably large” area are listed. The definition of “reasonably large area” is here set to the level 3 areas (here named *botanical countries*) of Brummitt (2001). Appendix 1 lists all checklists known to us that cover one or more of the botanical countries or larger areas. The boundaries between botanical countries mostly follow geopolitical boundaries. However, very large countries, such as Russia, China, and Brazil, are subdivided into administrative units or groups of administrative units. Countries containing geographically well-delimited areas such as the large islands of Borneo, Sumatra, and Corsica, are recognized separately. Very small countries, such as Liechtenstein, Vatican City, and Monaco, are merged with larger neighbors. In some cases, where there is no good recent checklist for the botanical country, checklists for a subdivision of them are included. Likewise, checklists that do not use the same geographical units that we use here are included only if they cover areas without a recent checklist. Only checklists that cover all species in the region are included, except in a few cases where there is no complete checklist, or when a series of papers together form a checklist.

Although there are checklists for many areas, substantial portions of the globe either lack lists entirely, or lack recent lists (Fig. 1). Notable is the lack of lists for the Caribbean Islands, Mexico, most of Central America, and for southernmost

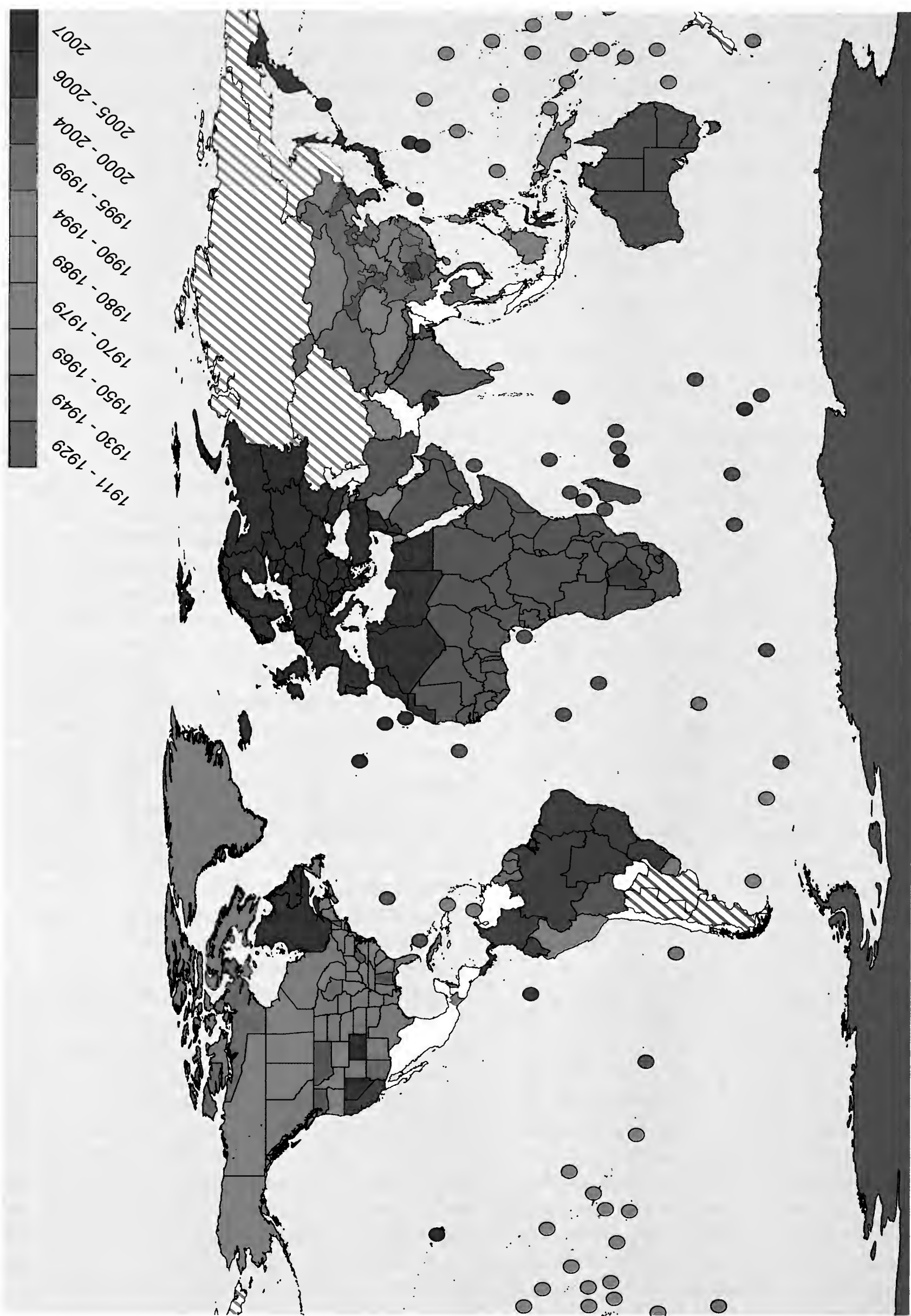


FIG. 1. Map indicating the year the latest checklist was published for a botanical country, and for subdivisions within a botanical country, if a more recent checklist exists for that part. Hatched areas only have checklists using larger units. White areas lack checklists or have only incomplete checklists. Small islands, for which checklists exist, are denoted by colored dots to make them visible.

South America. There are, in addition, no detailed checklists of the Asiatic part of the former Soviet Union, because the list by Kontantinova et al. (1992) uses much larger subdivisions than our botanical countries do. Two general areas also are notable as having mainly very old lists: Southeast Asia (cf. also Söderström & Sêneca, 2008) and North America.

Conclusion

Checklists remain an indispensable tool for setting priorities for conservation action, ecological research, and taxonomic and systematic studies. Broader participation by taxonomic specialists and regional experts will lead to checklists containing high quality data. Key elements that should be included in a checklist include: author citation, original citations, type data, synonymy (including differentiation between homonyms and heterotypic synonyms), distribution, and if not the direct citation of exemplar voucher specimens, then minimally a citation of the source for the record.

Acknowledgments

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APPENDIX I

The list includes all checklists published since 1900, known to us, that fulfill our criteria as covering a botanical country or larger area, and including all liverwort species. In some cases where there is no good recent checklist, we have loosened our requirements. When there is a newer checklist for a smaller part of the botanical country, we have included it (but not if it is older than the newest for the botanical country and thus assumed to be incorporated there). Also, when there is no good checklist covering all species, we have included lists that cover a larger part of the flora, e.g., all leafy liverworts of Mexico. In addition, we have included lists that comprise full updates of earlier lists without repeating the whole list.

We separate different kinds of checklists according to the following typography, although it sometimes is difficult to understand the background of the list. **Bold** = Specimen based, ***Bold Italic*** = cite specimens, Normal = literature based, *Normal Italic* = cite original literature, + = additional reports (only additions fully updating an earlier checklist), * = only covering part of the territory (see literature list for explanation), ° = only covering part of the species (see literature list for an explanation).

EUROPE

Müller 1910–1916, 1951–1958, Grolle 1976, Grolle 1983, Frey et al. 1995, Grolle & Long 2000.

NORTHWESTERN EUROPE

BRITAIN: Corley & Hill 1981, Düll 1983, Smith 1990, Hill et al. 1991, Blockeel & Long 1998, 1999,

Paton 1999, Schumacker & Vána 2000, Söderström et al. 2002b, Schumacker & Vána 2005, Söderström et al. 2007+. **DENMARK**: Jensen 1915, Arnell 1928, 1956, Damsholt et al. 1969, Düll 1983, Söderström 1995, Schumacker & Vána 2000, Damsholt 2002, Söderström et al. 2002a, b, Schumacker & Vána 2005, Söderström et al. 2007+. **FAEROE IS**: Boesen et al. 1976, Düll 1983, Söderström 1995, Schumacker & Vána 2000, Damsholt 2002, Söderström et al. 2002a, b, Schumacker & Vána 2005, Söderström et al. 2007+. **FINLAND**: Buch 1936, Arnell 1928, 1956, Koponen et al. 1977, Düll 1983, Söderström 1995, Schumacker & Vána 2000, Damsholt 2002, Söderström et al. 2002a, b, Schumacker & Vána 2000, Ulvinen et al. 2002, Schumacker & Vána 2005, Söderström et al. 2007+. **ICELAND**: Hesselbo 1918, Düll 1983, Jóhannsson 1983, Söderström 1995, Jóhannsson 1998–2003, Schumacker & Vána 2000, Damsholt 2002, Söderström et al. 2002a, b, Schumacker & Vána 2005, Söderström et al. 2007+. **IRELAND**: Corley & Hill 1981, Düll 1983, Smith 1990, Hill et al. 1991, Blockeel & Long 1998, 1999, Paton 1999, Schumacker & Vána 2000, Söderström et al. 2002b, Schumacker & Vána 2005, Hallingbäck et al. 2006, Söderström et al. 2007+, *Holyoak* 2003. **NORWAY**: Jørgensen 1934, Arnell 1928, 1956, Düll 1983, Frisvoll et al. 1984, 1995, Söderström 1995, Schumacker & Vána 2000, Damsholt 2002, Söderström et al. 2002a, b, Schumacker & Vána 2005, Söderström et al. 2007+. **SVALBARD**: Düll 1983, Frisvoll et al. 1995, Söderström 1995, Damsholt 2002, Schumacker & Vána 2000, Söderström et al. 2002a, b, Schumacker & Vána 2005, Söderström et al. 2007+. **SWEDEN**: Arnell 1928, 1956, Düll 1983, Hallingbäck & Söderström 1987, Söderström et al. 1992, Söderström 1995, Söderström & Hedenäs 1998, Schumacker & Vána 2000, Damsholt 2002, Söderström et al. 2002a, b, Schumacker & Vána 2005, Hallingbäck et al. 2006, Söderström et al. 2007+.

MIDDLE EUROPE

AUSTRIA: Düll 1983, Schumacker & Vána 2000, Söderström et al. 2002b, Schumacker & Vána 2005, Söderström et al. 2007+. **BELGIUM**: Düll 1983, Schumacker et al. 1985, Schumacker & Vána 2000, Sotiaux & Vandenpoorten 2001, Söderström et al. 2002b, Schumacker & Vána 2005, Söderström et al. 2007+. **CZECH REPUBLIC**: Düll 1983*, Vána 1997a, b¹, 1998, Schumacker & Vána 2000, Söderström et al. 2002b, Schumacker & Vána 2005, Söderström et al. 2007+, Kučera &

¹ Species erroneously reported.

Váňa 2003, 2005. **GERMANY:** Düll 1972, Düll 1983, Frahm & Frey 1983, Düll & Meinunger 1989, Ludwig et al. 1996, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, *Söderström et al. 2007⁺*. **HUNGARY:** Boros 1968, Düll 1983, Orbán & Vajda 1983, Schumacker & Váňa 2000, Söderström et al. 2002b, Erzberger & Papp 2004, Schumacker & Váňa 2005, *Söderström et al. 2007⁺*. **NETHERLANDS:** Gradstein 1977, Landwehr 1980, Margadant & During 1982, Düll 1983, Dirkse et al. 1989, 1999, **Gradstein & Melick 1996**, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Siebel et al. 2005, *Söderström et al. 2007⁺*. **POLAND:** *Szweykowski 1958*, Rejment-Grochowska 1966, 1971, Düll 1983, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, *Szweykowski 2006*, *Söderström et al. 2007⁺*. **SLOVAKIA:** Düll 1983^{*}, Kubinská et al. 1993, Váňa 1997b², Marhold & Hindák 1998, Schumacker & Váňa 2000, Kubinská et al. 2001, Söderström et al. 2002b, Schumacker & Váňa 2005, *Söderström et al. 2007⁺*. **SWITZERLAND:** **Meylan 1924**, Düll 1983, Schumacker & Váňa 2000, Söderström et al. 2002b, Schnyder et al. 2004, Schumacker & Váňa 2005, *Söderström et al. 2007⁺*.

SOUTHWESTERN EUROPE

BALEARES: Boesen 1976, Düll 1983, Sérgio et al. 1994, Casas 1998, Schumacker & Váňa 2000, Söderström et al. 2002b, Casas et al. 2004, Schumacker & Váňa 2005, Ros et al. 2007, *Söderström et al. 2007⁺*. **CORSICA:** Augier 1966, **Bischler & Jovet-Ast 1973**, Düll 1983, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Ros et al. 2007, *Söderström et al. 2007⁺*, *Sotiaux et al. 2007*. **FRANCE:** Augier 1966, Düll 1983, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Ros et al. 2007, *Söderström et al. 2007⁺*. **PORTUGAL:** **Casares-Gil 1919**, **Machado Guimarães 1925**, Sabino de Freitas 1944, Düll 1983, Sérgio et al. 1994, Schumacker & Váňa 2000, Söderström et al. 2002b, *Sérgio & Carvalho 2003*, Schumacker & Váňa 2005, Ros et al. 2007, Sérgio et al. 2007, *Söderström et al. 2007⁺*. **SARDINIA:** Zodda 1934, **Bischler & Jovet-Ast 1972**, Düll 1983, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Ros et al. 2007, *Söderström et al. 2007⁺*. **SPAIN:** **Casares-Gil 1919**, Düll 1983, Sérgio et al. 1994, Casas 1998, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa

2005, Ros et al. 2007, Sérgio et al. 2007, *Söderström et al. 2007⁺*.

SOUTHEASTERN EUROPE

ALBANIA: Düll 1983, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Colacino & Sabovljević 2006, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **BULGARIA:** **Petrov 1975**, Düll 1983, Ganeva & Düll 1999, Schumacker & Váňa 2000, Söderström et al. 2002b, **Ganeva & Natcheva 2003**, Schumacker & Váňa 2005, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **BOSNIA-HERZEGOVINA:** **Pavletić 1955, 1968**, Söderström et al. 2002b, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **CRETE:** **Düll 1979**, *Preston 1981*, Düll 1983, *Preston 1984⁺*, **Düll 1995**, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Ros et al. 2007, *Söderström et al. 2007⁺*. **CROATIA:** **Pavletić 1955, 1968**, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **GREECE:** *Preston 1981*, Düll 1983, *Preston 1984⁺*, **Düll 1995**, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Sabovljević & Natcheva 2006^{*}, Ros et al. 2007, *Söderström et al. 2007⁺*. **ITALY:** Zodda 1934, Düll 1983, Aleffi & Schumacker 1995, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Aleffi 2005, Ros et al. 2007, *Söderström et al. 2007⁺*. **MACEDONIA:** **Pavletić 1955, 1968**, Söderström et al. 2002b, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **MONTENEGRO:** **Pavletić 1955, 1968**, *Sabovljević 2000*, Söderström et al. 2002b^{*}, Sabovljević et al. 2004, *Dragičević & Veljić 2006*, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **ROMANIA:** Papp 1967, **Mohan 1971**, Düll 1983, Mihai 1983, **Mohan 1984, 1998**, Schumacker & Váňa 2000, Söderström et al. 2002b, *Ștefanuț 2002*, Schumacker & Váňa 2005, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **SERBIA:** **Pavletić 1955, 1968**, *Sabovljević 2000*, Söderström et al. 2002b^{*}, Sabovljević et al. 2004, Sabovljević & Natcheva 2006, Ros et al. 2007, *Söderström et al. 2007⁺*. **SICILY:** Zodda 1934, Düll 1983, *Dia et al. 1985*, Aleffi & Schumacker 1995, Schumacker & Váňa 2000, Söderström et al. 2002b, Schumacker & Váňa 2005, Ros et al. 2007, *Söderström et al. 2007⁺*. **SLOVENIA:** **Pavletić 1955, 1968**, Söderström et al. 2002b, Sabovljević & Natcheva 2006, Ros

² Species erroneously reported.

et al. 2007, *Söderström et al. 2007⁺*. **TURKEY-IN-EUROPE**: *Gökler & Öztürk 1996*, Schumacker & Váňa 2000, *Söderström et al. 2002b*, Schumacker & Váňa 2005, Sabovljević & Natcheva 2006, *Söderström et al. 2007⁺*. **YUGOSLAVIA (IN ITS FORMER EXTENT)**: Düll 1983, Schumacker & Váňa 2000, 2005.

EASTERN EUROPE

Düll 1983[•], Konstantinova et al. 1992[•], Konstantinova & Potemkin 1996[•], Schumacker & Váňa 2000[•], 2005[•].

BELARUS: *Söderström et al. 2002b, 2007⁺*. **CRIMEA**: *Zerov 1958*, Düll 1983, Schumacker & Váňa 2000, *Söderström et al. 2002b*, **Partyka 2005**, Schumacker & Váňa 2005, *Söderström et al. 2007⁺*. **ESTONIA**: Ingerpuu et al. 1994, Ingerpuu & Vellak 1998, *Vellak et al. 2001⁺*, *Söderström et al. 2002a, b, Vellak et al. 2006⁺*, *Söderström et al. 2007⁺*. **KALININGRAD**: *Söderström et al. 2002b, 2007⁺*. **KAZACHSTAN-IN-EUROPE**: *Söderström et al. 2002b, 2007⁺*. **LATVIA**: Āboliņa 1984, 2001, *Söderström et al. 2002a, b, 2007⁺*. **LITHUANIA**: Najaulis et al. 1995, *Söderström et al. 2002a, b, 2007⁺*. **MOLDOVO**: *Abramova & Abramov 1966*, Simonov 1972, *Söderström et al. 2002b, 2007⁺*. **RUSSIA CENTRAL**: *Söderström et al. 2002b, 2007⁺*. **RUSSIA EAST**: *Söderström et al. 2002b, 2007⁺*. **RUSSIA NORTH**: Schljakov 1976–1982, *Söderström et al. 2002b, 2007⁺*. **RUSSIA NORTHWEST**: *Söderström et al. 2002b, 2007⁺*. **RUSSIA SOUTH**: *Söderström et al. 2002b, 2007⁺*. **UKRAINE**: *Zerov 1939[•]*, Váňa & Virchenko 1993[•], *Söderström et al. 2002b, 2007⁺*.

AFRICA

NORTH AFRICA

ALGERIA: Trabut 1942, **Jelenc 1950**, *Ros et al. 1999*, *Ros et al. 2007*. **EGYPT**: Trabut 1942, **Jelenc 1950**, *Jovet-Ast & Bischler 1970*, *Ros et al. 1999*, *Ros et al. 2007[•]*. **LIBYA**: Trabut 1942, **Jelenc 1950**, *Jovet-Ast & Bischler 1969*, *Ros et al. 1999*, *Ros et al. 2007*. **MOROCCO**: Trabut 1942, **Jelenc 1950**, *Jovet-Ast 1955–1956*, *Ros et al. 1999*, *Ros et al. 2007*. **TUNISIA**: Trabut 1942, **Jelenc 1950**, *Jovet-Ast & Bischler 1972*, *Ros et al. 1999*, *Ros et al. 2007*. **WESTERN SAHARA**: *Ros et al. 1999*, *Ros et al. 2007*.

MACARONESIA

AZORES: *Eggers 1982*, Düll 1983, Schumacker & Váňa 2000, Schumacker 2001, Sjögren 2001, *Söderström et al. 2002b*, *Frahm 2005*, *Gabriel et al. 2005*, Schumacker & Váňa 2005, *Frahm & Häusler 2007*, *Söderström et al. 2007⁺*. **CANARY IS**: *Eggers 1982*, Düll 1983, **Dirkse et al. 1993**,

Schumacker & Váňa 2000, *Söderström et al. 2002b*, Schumacker & Váňa 2005, *Frahm & Häusler 2007*, *Ros et al. 2007*, *Söderström et al. 2007⁺*. **CAPE VERDE IS**: *Eggers 1982*, Muhle 1986, *Frahm et al. 1996*, *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **MADEIRA**: *Eggers 1982*, Düll 1983, Schumacker & Váňa 2000, *Söderström et al. 2002b*, Schumacker & Váňa 2005, *Frahm & Häusler 2007*, *Ros et al. 2007*, *Söderström et al. 2007⁺*.

WEST TROPICAL AFRICA

BENIN: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **BURKINA FASSO**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **GAMBIA**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **GHANA**: *Jones & Harrington 1983*, *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **GUINEA**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **GUINEA-BISSAU**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **IVORY COAST**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **LIBERIA**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **MALI**: *Wigginton & Grolle 1996*, *Ros et al. 1999*, *Wigginton 2002, 2004*. **MAURETANIA**: *Wigginton & Grolle 1996*, *Ros et al. 1999*, *Wigginton 2002, 2004*. **NIGER**: *Wigginton & Grolle 1996*, *Ros et al. 1999*, *Wigginton 2002, 2004*. **NIGERIA**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **SENEGAL**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **SIERRA LEONE**: *Jones & Harrington 1983*, *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **TOGO**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*.

WEST-CENTRAL TROPICAL AFRICA

BURUNDI: *Demaret 1942*, *Fischer 1993*, *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **CABINDA**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **CAMEROON**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **CENTRAL AFRICAN REPUBLIC**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **CONGO**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **EQUATORIAL GUINEA**: *Wigginton & Grolle 1996*, *Heras & Infante 1996*, 2001, *Wigginton 2002, 2004*. **GABON**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **GUINEA GULF ISLANDS**: *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **RWANDA**: *Demaret 1942*, *Fischer 1993*, *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*. **ZAIRE**: *Demaret 1942*, *Fischer 1993*, *Wigginton & Grolle 1996*, *Wigginton 2002, 2004*.

NORTHEAST TROPICAL AFRICA

CHAD: *Wigginton & Grolle 1996*, *Ros et al. 1999*, *Wigginton 2002, 2004*. **DJIBOUTI**: *Cufodontis*

1952, Wigginton & Grolle 1996, Wigginton 2002, 2004. ERITREA: Cufodontis 1952, Wigginton & Grolle 1996, Wigginton 2002, 2004. ETHIOPIA: Cufodontis 1952, Wigginton & Grolle 1996, Wigginton 2002, 2004. SOCOTRA: Jones 1969, Frey & Kürschner 1988, Mies 1994, Wigginton & Grolle 1996, Kürschner 2000, Wigginton 2002, 2004. SOMALIA: Cufodontis 1952, Wigginton & Grolle 1996, Wigginton 2002, 2004. SUDAN: Wigginton & Grolle 1996, Wigginton 2002, 2004.

EAST TROPICAL AFRICA

KENYA: Wigginton & Grolle 1996, Wigginton 2002, Chuah-Petiot 2003, Wigginton 2004. TANZANIA: Wigginton & Grolle 1996, Wigginton 2002, 2004. UGANDA: Wigginton & Grolle 1996, Wigginton 2002, 2004.

SOUTH TROPICAL AFRICA

ANGOLA: Wigginton & Grolle 1996, Wigginton 2002, 2004. MALAWI: O'Shea 1993, Wigginton & Grolle 1996, Wigginton 2002, 2004. MOZAMBIQUE: Wigginton & Grolle 1996, Wigginton 2002, 2004. ZAMBIA: Wigginton & Grolle 1996, Wigginton 2002, 2004. ZIMBABWE: Sim & Dixon 1922, Best 1990, Wigginton & Grolle 1996, Wigginton 2002, 2004, Manyanga & Perold 2004.

SOUTHERN AFRICA

BOTSWANA: Perold & Van Rooy 1993, Wigginton & Grolle 1996, Wigginton 2002, Wigginton 2004, Setshogo 2005. CAPE PROVINCES: Perold & Van Rooy 1993, Perold 2003. FREE STATE: Perold & Van Rooy 1993, Perold 2003. LESOTHO: Arnell 1963, Perold & Van Rooy 1993, Wigginton & Grolle 1996, Wigginton 2002, 2004, Perold 2003, Kobisi 2005. NAMIBIA: Russell & Van Rooy 1988, Perold & Van Rooy 1993, Wigginton & Grolle 1996, Wigginton & Grolle 1996, Craven 1999, Wigginton 2002, Perold 2003, Wigginton 2004. NATAL: Perold & Van Rooy 1993, Perold 2003. SOUTH AFRICA: Sim 1916, 1926, Arnell 1963, Magill & Schelpe 1979, Wigginton & Grolle 1996, Wigginton 2002, 2004. SWAZILAND: Arnell 1963, Perold & Van Rooy 1993, Wigginton & Grolle 1996, Wigginton 2002, Perold 2003, Wigginton 2004, Braun et al. 2004. TRANSVAAL: Perold & Van Rooy 1993, Perold 2003.

MIDDLE ATLANTIC OCEAN

ASCENSION: Grolle 1988, Wigginton & Grolle 1996, Wigginton 2002, 2004. ST HELENA: Wigginton & Grolle 1996, Wigginton 2002, 2004.
Western Indian Ocean

ALDABRA: Grolle 1995, Seaward et al. 1996, Wigginton 2002, 2004. CHAGOS: Grolle 1995, Wigginton 2002, 2004, Seaward et al. 2006. COMORES: Grolle 1995, Wigginton 2002, 2004. MADAGASCAR: Jovet-Ast 1949, Grolle 1995, Wigginton 2002, 2004. MAURITIUS: Grolle 1995, Wigginton 2002, 2004. MOZAMBIQUE CHANNEL ISLANDS: Wigginton 2002, 2004. RÉUNION: Grolle 1995, Wigginton 2002, 2004, Ah-Peng & Bardat 2005. RODRIGUEZ: Grolle 1995, Wigginton 2002, 2004. SEYCHELLES: Grolle 1978, 1995, Wigginton 2002, 2004.

TEMPERATE ASIA

Konstantinova & Potemkin 1996*.

SIBERIA

ALTAY: Váňa & Ignatov 1995. BURYATIYA: X. CHITA: X. IRKUTSK: X. KRASNOYARSK: X. TUVA: X. WEST SIBERIA: X. [FRANZ JOSEF LAND: Söderström et al. 2002b, 2007*. NOVAYA ZEMLYA: Söderström et al. 2002b, 2007*. SEVERNAYA ZEMLYA: Potemkin 2000]. YAKUTSK: X.

RUSSIAN FAR EAST

AMUR: X. KAMCHATKA: Bakalin 2003, 2005. KHABAROVSK: X. KURIL IS: Nyushko & Potemkin 2005. MAGADAN: X. [CHUKOTKA: Abramova et al. 1985]. PRIMORYE: X. SAKHALIN: Kitagawa 1963, Bakalin et al. 2005, Nyushko & Potemkin 2005.

MIDDLE ASIA

Konstantinova et al. 1992.

KAZACHSTAN: X. KIRGIZSTAN: X. TADZHIKISTAN: X. TURKMENISTAN: X. UZBEKISTAN: X.

CAUCASUS

ARMENIA: Abramova & Abramov 1959, Manakyan 1995. AZERBAJDZHAN: X. GRUZIYA: Czikovani 1986, Czikovani & Svanidze 2004. NORTH CAUCASUS: Söderström et al. 2002b, 2007*.

WESTERN ASIA

AFGHANISTAN: Kitagawa 1964, Frey 1974, Frey & Kürschner 1991. CYPRUS: Frey & Kürschner 1991, Ros et al. 2007. IRAN: Frey 1974, Frey & Kürschner 1991, Akhani & Kürschner 2004. IRAQ: Frey & Kürschner 1991. ISRAEL: Jovet-Ast & Bischler 1966, Frey & Kürschner 1991, Ros et al. 2007. JORDAN: El-Oqlah et al. 1988, Frey & Kürschner 1991, Ros et al. 2007. LEBANON: Frey & Kürschner 1991, Ros et al. 2007. SINAI: Jovet-Ast & Bischler 1970, Frey & Kürschner 1991. SYRIA: Frey & Kürschner 1991, Ros et al. 2007. TURKEY: Henderson 1961, Henderson & Prentice 1969,

Gökler et al. 1985, Çetin 1988, Frey & Kürschner 1991, Gökler & Öztürk 1991, Kürschner & Erdağ 2005, Ros et al. 2007*.

ARABIAN PENINSULA

BAHREIN: Frey & Kürschner 1988, Frey & Kürschner 1991, Kürschner 2000. **KUWAIT:** Frey & Kürschner 1988, Frey & Kürschner 1991, Kürschner 2000. **OMAN:** Long 1987, Frey & Kürschner 1988, Frey & Kürschner 1991, Kürschner 2000. **QUATAR:** Frey & Kürschner 1988, Frey & Kürschner 1991, Kürschner 2000. **SAUDI ARABIA:** Long 1987, Frey & Kürschner 1988, Frey & Kürschner 1991, Kürschner 2000. **UNITED ARAB EMIRATES:** Long 1987, Frey & Kürschner 1988, Frey & Kürschner 1991, Kürschner 2000. **YEMEN:** Long 1987, Frey & Kürschner 1988, Frey & Kürschner 1991, Kürschner 2000.

CHINA

CHINA CENTRAL: Piippo 1990a. [**GUIZHOU:** Zhang & Chen 2006. **HUBEI:** Peng et al. 2000. **SICHUAN:** Piippo et al. 1997. **YUNNAN:** Piippo et al. 1998, Gao & Cao 2001]. **CHINA NORTH-CENTRAL:** Piippo 1990a. [**GANSU:** Wu et al. 2002. **SHANDONG:** Zhao & Cao 1998]. **CHINA SOUTHEAST:** Piippo 1990a. **GUANGXI:** Zhu & So 2003. **HONG KONG:** So 1995, Zhu & So 1996, Zhang & Lin 1997, Zhang 2003. **HUNAN:** Rao et al. 1997. **JIANGXI:** Fang et al. 1998. **ZHEJIANG:** Zhu et al. 1998]. **HAINAN:** Piippo 1990a, Lin et al. 1994. **INNER MONGOLIA:** Piippo 1990a. [**NEI MONGOL:** Bai 1993, Bai & Zhao 1996]. **MANCHURIA:** Gao & Chang 1981, Piippo 1990a. [**JILIN:** Söderström 2000]. **QUINHAI:** Piippo 1990a. **TIBET (XIZANG):** Li 1985, Piippo 1990a. **XINJIANG:** Piippo 1990a, Whittemore et al. 1998.

MONGOLIA

MONGOLIA: Abramova & Abramov 1983.

EASTERN ASIA

Mizutani & Hattori 1969*, Furuki & Mizutani 1994*, 1995*, 2004*.

BONIN IS: Miller 1960, Inoue & Iwatzuki 1969, Inoue 1970, Miller et al. 1983, Yamada & Iwatsuki 2006. **JAPAN:** Yamada & Iwatsuki 2006. **KOREA:** Choe & Yamada 1974, Choe 1980, Choe & Choi 1980, Kim 1991, Yamada & Choe 1997, Hong 1998, 2003. **RYUKYU IS:** Shin 1968, 1970a, b, Yamada & Iwatsuki 2006. **TAIWAN:** Yang 1960, Lai & Wang-Yang 1976, Kuo & Chang 1988, Piippo 1990a, Lin 2000. **VOLCANO IS:** Miller 1960, Inoue & Iwatzuki 1969, Inoue 1970, Miller et al. 1983, Furuki 1997, Yamada & Iwatsuki 2006.

TROPICAL ASIA

INDIAN SUBCONTINENT

³Kachroo 1969–1973, Parihar 1962, Kachroo et al. 1977, 1994, Bapna & Kachroo 2000.

ASSAM: X. **BANGLADESH:** Banu-Fattah 2001. **EAST HIMALAYA:** Chopra 1943. [**BHUTAN:** Long 1979, Long & Grolle 1990]. **INDIA:** Chopra 1943. [**CHANDIGARGH:** Kashyap 1929, 1932, Kashyap & Chopra 1932. **GUJARAT:** Mahabale & Chavan 1954, Chaudhary et al. 2006. **HARYANA:** Kashyap 1929, 1932, Kashyap & Chopra 1932. **KERALA:** Easa 2003. **PUNJAB:** Kashyap 1929, 1932, Kashyap & Chopra 1932. **UTTAR PRADESH:** Kashyap 1929, 1932, Kashyap & Chopra 1932]. **LACCADIVES:** X. **MALDIVES:** X. **NEPAL:** Chopra 1943, Grolle 1966, 1974+, Kattel 2002. **PAKISTAN:** Kashyap 1929*, 1932*, Kashyap & Chopra 1932*. **SRI LANKA:** Abeywickrama 1959, Abeywickrama & Jansen 1978, Onraedt 1981+. **WEST HIMALAYA:** Kashyap 1929, 1932, Kashyap & Chopra 1932. [**HIMACHAL PRADESH:** Kashyap 1929, 1932, Kashyap & Chopra 1932. **KASHMIR:** Kashyap 1929, 1932, Kashyap & Chopra 1932, Srivastava 1979. **UTTARANCHAL:** Kashyap 1929, 1932, Kashyap & Chopra 1932].

INDO-CHINA

ANDAMAN: X. **CAMBODJA:** X. **LAOS:** X. **MYANMAR:** X. **NICOBAR IS:** X. **SOUTH CHINA SEA:** X. **THAILAND:** Sornsamran & Thaithong 1995. **VIETNAM:** Pócs 1965, Pócs et al. 1967*.

MALESIA

BORNEO: Menzel 1988. **CHRISTMAS I:** X. **COCOS I:** X. **JAWA:** Schiffner 1900°. **LESSER SUNDA IS:** X. **MALAYA:** X. [**SINGAPORE:** Piippo et al. 2002]. **MOLUCCAS:** X. **PHILIPPINES:** Tan & Engel 1986. **SUMATRA:** X. **SULAWESI:** Gradstein et al. 2005, Aryanti & Gradstein 2007*.

PAPUASIA

BISMARCK ARCHIPELAGO: Miller et al. 1983, Grolle & Piippo 1984a. **NEW GUINEA**⁴: Piippo 1984a, b, Grolle & Piippo 1984a, b, Piippo 1985a, b, c, Grolle & Piippo 1986, Hattori & Piippo 1986, Piippo 1988a, b, c, 1989a, b, Váňa & Piippo 1989a, b, Yamada & Piippo 1989, Piippo 1990b, Grolle & Piippo 1990, Bischler & Piippo 1991, Piippo 1991a,

³ These references treat species reported from India but do not always clearly separate between peninsular India, Himalaya, Assam, and the Andaman and Nicobar Is.

⁴ The series of papers from the Huon Peninsula of Papua New Guinea will, when finished, be a full flora with specimens cited. All parts so far issued are cited here.

b, c, Pócs et al. 1994, 1995, Pócs & Piippo 1999. **SOLOMON IS:** Miller et al. 1983, *Grolle & Piippo 1984a.*

AUSTRALASIA

AUSTRALIA

LORD HOWE I: Miller et al. 1983. **NEW SOUTH WALES:** Scott & Bradshaw 1985, McCarthy 2003. **NORFOLK IS:** Henderson & Prentice 1971, Miller et al. 1983. **NORTHERN TERRITORY:** Scott & Bradshaw 1985, McCarthy 2003. **QUEENSLAND:** Bailey 1913, Scott & Bradshaw 1985, Windolf 1987, McCarthy 2003. **SOUTH AUSTRALIA:** Scott & Bradshaw 1985, Bolin & Henderson 2002, McCarthy 2003. **TASMANIA:** Rodway 1917, Scott & Bradshaw 1985, Ratkowsky 1987, Moscal & Kirkpatrick 1997, McCarthy 2003. **VICTORIA:** Scott & Bradshaw 1985, Cropper et al. 1991, McCarthy 2003. **WESTERN AUSTRALIA:** Scott & Bradshaw 1985, McCarthy 2003.

NEW ZEALAND

Hamlin 1972⁺, 1973⁺, 1975⁺, Glenney 1998⁺.

ANTIPODEAN IS: Hodgson 1962. **CHATHAM I:** Hodgson 1962. **KERMADEC IS:** Campbell 1977, Miller et al. 1983. **NORTH I:** X. **SOUTH I:** X.

PACIFIC

SOUTHWESTERN PACIFIC

FIJI: Miller et al. 1983. **GILBERT IS:** Miller 1960, Miller et al. 1963, 1983. **HOWLAND–BAKER IS:** Miller et al. 1983. **NAURU:** Miller et al. 1983. **NEW CALEDONIA:** Miller et al. 1983. **NIUE:** Campbell 1970, Miller et al. 1983. **PHOENIX IS:** Miller et al. 1983. **SAMOA:** Grolle & Schultze-Motel 1973, Grolle 1980⁺, Miller et al. 1983. **SANTA CRUZ IS:** Miller et al. 1983. **TOKELAU–MANIHIKI:** Miller et al. 1983. **TONGA:** Fulford 1959, Miller et al. 1983. **TUVALU:** Miller et al. 1983. **VANUATU:** Miller et al. 1983. **WALLIS–FUTUNA IS:** Miller et al. 1983.

SOUTHEASTERN PACIFIC

COOK IS: Miller et al. 1983. **EASTER IS:** Miller et al. 1983, Grolle 2002b, 2002c⁺. **LINE ISLANDS:** Miller et al. 1983. **MARQUESAS:** Miller et al. 1983. **PITCAIRN IS:** Miller et al. 1983. **SOCIETY IS:** Miller et al. 1983, Whittier & Whittier 1987. **TUAMOTU IS:** Miller et al. 1983. **TUBUAI IS:** Miller et al. 1983.

NORTHWESTERN PACIFIC

MARCUS IS: Miller et al. 1963, 1983. **MARIANA IS:** Miller 1960, Miller et al. 1963, 1983. **MARSHALL IS:** Miller 1960, Miller et al. 1963, 1983. **MICRONESIAN FEDERATE STATE:** Miller 1960, Miller et al. 1963, 1983. **PALAU:** Miller 1960,

Miller et al. 1963, Swanson & Miller 1969, Miller et al. 1983. **WAKE IS:** Miller et al. 1963, 1983.

NORTHEASTERN PACIFIC

HAWAII: Miller et al. 1983, Staples & Imada 2007.

NORTH AMERICA

Evans 1940, Stotler & Crandall-Stotler 1977.

SUBARCTIC NORTH AMERICA

ALASKA: Frye & Clark 1937–1947, Eyerdam 1952, Worley 1970⁺, Steere & Inoue 1978⁺. **ALEUTIAN IS:** Eyerdam 1952. **GREENLAND:** Frye & Clark 1937–1947, Schuster 1966–1992, Schuster & Damsholt 1974⁺, Schuster 1988⁺. **NORTHWEST TERRITORIES:** Macoun 1902, Frye & Clark 1937–1947. **NUNAVUT:** Macoun 1902, Frye & Clark 1937–1947, Polunin 1947, Schuster 1966–1992. **YUKON:** Macoun 1902, Evans 1903a, Frye & Clark 1937–1947, Hong & Vitt 1977.

WESTERN CANADA

ALBERTA: Macoun 1902, Brinkman 1923a, Frye & Clark 1937–1947, Bird & Hong 1975, Johnson 1989⁺. **BRITISH COLUMBIA:** Macoun 1902, Brinkman 1923b, Frye & Clark 1937–1947, Schofield 1968. **MANITOBA:** Macoun 1902, Frye & Clark 1937–1947, Lowe 1943, Schuster 1966–1992, Johnson 1989⁺. **SASKATCHEWAN:** Macoun 1902, Frye & Clark 1937–1947, Conard 1957, Johnson 1989⁺.

EASTERN CANADA

LABRADOR: Macoun 1902, Frye & Clark 1937–1947, Schuster 1966–1992, Brassard & Williams 1976, Favreau & Brassard 1988, Faubert 2007. **NEW BRUNSWICK:** Macoun 1902, Frye & Clark 1937–1947, Schuster 1966–1992. **NEWFOUNDLAND:** Macoun 1902, Frye & Clark 1937–1947, Buch & Tuomikoski 1955, Schuster 1966–1992. **NOVA SCOTIA:** Macoun 1902, Nichols 1916, Brown 1929⁺, 1936, Frye & Clark 1937–1947, Brown 1946⁺, 1951⁺, Williams & Cain 1959⁺, Schuster 1966–1992. **ONTARIO:** Macoun 1902, Frye & Clark 1937–1947, Cain & Fulford 1948, Schuster 1966–1992. **QUEBEC:** Macoun 1902, Frye & Clark 1937–1947, Lepage 1944–1945, 1960, Schuster 1966–1992, Favreau & Brassard 1988, Faubert 2007. **PRINCE EDWARD IS:** Macoun 1902, Frye & Clark 1937–1947, Schuster 1966–1992.

NORTHWESTERN UNITED STATES

COLORADO: Evans 1915, Frye & Clark 1937–1947, Weber 1963⁺, Weber & Johnson 1976, Weber & Wittmann 2007. **IDAHO:** Clark & Frye 1928, Frye & Clark 1937–1947, Hong 1976. **MONTANA:** Clark & Frye 1928, Frye & Clark 1937–1947,

Hong 1975^o, *1977b*^o, *Hong et al. 1998*, *Hong 2002a*. OREGON: *Clark & Frye 1928*, *Frye & Clark 1937–1947*, *Hong 1978*. WASHINGTON: *Clark & Frye 1928*, *Frye & Clark 1937–1947*, *Hong 2002b*. WYOMING: *Clark & Frye 1928*, *Porter 1933–1935*, *Frye & Clark 1937–1947*, *Hong 1977a*.

NORTH-CENTRAL UNITED STATES

ILLINOIS: *Hague 1937*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *McKnight 1987*, *Timme & Redfearn 1997*[•]. IOWA: *Frye & Clark 1937–1947*, *Conard 1942*, *1945*, *1956*, *Schuster 1966–1992*. KANSAS: *Frye & Clark 1937–1947*, *McGregor 1955*, *Schuster 1966–1992*. MINNESOTA: *Frye & Clark 1937–1947*, *Conklin 1942*, *Schuster 1953*, *Schuster 1966–1992*. MISSOURI: *Frye & Clark 1937–1947*, *Gier 1955*, *Redfearn 1964*⁺, *Schuster 1966–1992*, *Timme & Redfearn 1997*[•]. NEBRASKA: *Evans 1924*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Churchill & Redfearn 1978*. NORTH DAKOTA: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. OKLAHOMA: *Little 1936*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Timme & Redfearn 1997*[•]. SOUTH DAKOTA: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. WISCONSIN: *Conklin 1929*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Bowers & Freckman 1979*, *Lyman 1999*⁺.

NORTHEASTERN UNITED STATES

CONNECTICUT: *Evans 1903b*, *Evans & Nichols 1908*, *Evans 1913*, *Evans 1923*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*. INDIANA: *Frye & Clark 1937–1947*, *Parker 1938*, *Wagner 1946*⁺, *Schuster 1966–1992*. MAINE: *Evans 1903b*, *Evans 1913*, *Evans 1923*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*. MASSACHUSETTS: *Evans 1903b*, *Evans 1913*, *Evans 1923*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Mischler & Miller 1983*⁺. MICHIGAN: *Kaufmann 1915*, *Nichols 1922*, *1925*⁺, *1933*⁺, *1935*⁺, *1936*⁺, *Frye & Clark 1937–1947*, *Steere 1947*, *Schuster 1966–1992*, *Hollensen 1984*. NEW HAMPSHIRE: *Evans 1903b*, *Evans 1913*, *Evans 1923*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Cleavitt 2004*. NEW JERSEY: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. NEW YORK: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. OHIO: *Frye & Clark 1937–1947*, *Miller 1964*, *Schuster 1966–1992*. PENNSYLVANIA: *Porter 1904*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*. RHODE ISLAND: *Evans 1903b*, *Evans 1913*, *Evans 1923*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*. VERMONT: *Evans 1903b*, *Evans 1913*, *Evans 1923*, *Dole 1928*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *McQueen 1992*. WEST VIRGINIA: *Sheldon 1907*, *Frye & Clark 1937–1947*, *Ammons 1938*, *Ammons 1940*, *Schuster 1966–1992*, *Studlar et al. 2000*.

SOUTHWESTERN UNITED STATES

ARIZONA: *Evans 1917*, *Frye & Clark 1937–1947*. CALIFORNIA: *Frye & Clark 1937–1947*, *Doyle & Stotler 2006*. NEVADA: *Frye & Clark 1937–1947*, *Brinda et al. 2007*. UTAH: *Frye & Clark 1937–1947*, *Flowers 1945*, *1954*, *1961*.

SOUTH-CENTRAL UNITED STATES

NEW MEXICO: *Stanley 1915*, *1916*⁺, *Arsène 1933*, *Frye & Clark 1937–1947*, *Shields 1954*, *Bird 1960*⁺. TEXAS: *McAllister et al. 1932*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*.

SOUTHEASTERN UNITED STATES

ALABAMA: *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Timme & Bowers 2000*. ARKANSAS: *Frye & Clark 1937–1947*, *Wittlake 1954*, *Schuster 1966–1992*, *Timme & Redfearn 1997*[•]. DELAWARE: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. DISTRICT OF COLUMBIA: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. FLORIDA: *Frye & Clark 1937–1947*, *McFarlin 1940*, *Schuster 1966–1992*. GEORGIA: *Brown 1924*, *Frye & Clark 1937–1947*, *Jacobs 1954*, *Schuster 1966–1992*. KENTUCKY: *Fulford 1934*, *1936*⁺, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Snider et al. 1988*. LOUISIANA: *Frye & Clark 1937–1947*, *Koch 1961*, *Schuster 1966–1992*. MARYLAND: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. MISSISSIPPI: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. NORTH CAROLINA: *Blomquist 1936*, *Frye & Clark 1937–1947*, *Schuster 1966–1992*, *Hicks 1992*. SOUTH CAROLINA: *Frye & Clark 1937–1947*, *Schuster 1966–1992*. TENNESSEE: *Frye & Clark 1937–1947*, *Sharp 1939*[•], *Schuster 1966–1992*. VIRGINIA: *Frye & Clark 1937–1947*, *Patterson 1949*, *1950*⁺, *1951*⁺, *1955*⁺, *Schuster 1966–1992*.

MEXICO

Fulford & Sharp 1990^o.

MEXICAN PACIFIC IS.: X. [GUADELUPE: *Sutcliffe 1932*, *Crum & Miller 1956*]. MEXICO CENTRAL: X. MEXICO NORTHEAST: X. MEXICO NORTHWEST: X. MEXICO SOUTHEAST: X. [CHIAPAS: *Bourell 1992*]. MEXICO SOUTHWEST: X. VERACRUZ: X.

SOUTH AMERICA

CENTRAL AMERICA

BELIZE: *Whittemore & Allen 1996*. CENTRAL AMERICAN PACIFIC I.: X. [COCOS IS.: *Fosberg & Klawe 1966*, *Dauphin 1999*]. COSTA RICA: *Morales 1991*, *Gradstein 1999*[•], *Dauphin 2005*. EL SALVADOR: X. GUATEMALA: X. HONDURAS: X. NICARAGUA: X. PANAMA: *Stotler et al. 1998*, *Gradstein 1999*[•], *Dauphin et al. 2006*⁺.

CARIBBEAN

ARUBA: X. BAHAMAS: *Evans 1911*. BERMUDA: *Evans 1906*, *Evans 1918*. CAYMAN IS.: X. CUBA: *Grolle 1975⁺*. DOMINICAN REPUBLIC: X. HAITI: X. JAMAICA: X. LEEWARD IS.: X [GUADELOUPE: *Pagán 1942*, *Foucault 1977*. MONTSERRAT: *Casares-Gil 1905*. VIRGIN IS.: *Gradstein 1989*]. NETHERLANDS ANTILLES: *Van Slageren 1979*. PUERTO RICO: *Pagán 1939*, *Gradstein 1989*. SOUTHWEST CARRIBEAN: X. TRINIDAD–TOBAGO: X. TURKS–CAICOS IS.: X. VENEZUELAN ANTILLES: X. WINDWARD IS.: X [DOMINICA: *Fulford 1987^{+o}*. ST VINCENT: *Fulford 1984⁺*].

NORTHERN SOUTH AMERICA

FRENCH GUIANA: *Gradstein & Hekking 1989*, *Boggan et al. 1997*. GUYANA: *Gradstein & Hekking 1989*, *Boggan et al. 1997*. SURINAM: *Jovet-Ast 1957*, *Gradstein & Hekking 1989*, *Boggan et al. 1997*. VENEZUELA: *Gradstein 1999[•]*.

WESTERN SOUTH AMERICA

BOLIVIA: *Gradstein 1999[•]*, *Gradstein et al. 2003*. COLOMBIA: *Gradstein & Hekking 1979*, *Uribe & Gradstein 1998*, *Gradstein 1999[•]*, *Campos & Uribe 2006⁺*, *Gradstein et al. 2006*. ECUADOR: *Gradstein 1999[•]*, *León-Yáñez et al. 2006*. GALAPAGOS IS.: *Evans 1902*, *Weber 1966*, *Weber 1976⁺*, *Gradstein & Weber 1982*, *Gradstein 1995*, *León-Yáñez et al. 2006*. PERU: *Menzel 1984*, *Gradstein 1999[•]*.

BRAZIL

BRAZIL NORTH: *Yano 1984*, *1989⁺*, *1996a⁺*, *b*, *Gradstein & Costa 2003*, *Yano 2006 a⁺*, *b⁺*. BRAZIL NORTHEAST: *Yano 1984*, *1989⁺*, *1996a⁺*, *b*, *Gradstein & Costa 2003*, *Yano 2006 a⁺*, *b⁺*. BRAZIL SOUTH: *Yano 1984*, *1989⁺*, *1996a⁺*, *b*, *Gradstein & Costa 2003*, *Yano 2006 a⁺*, *b⁺*. BRAZIL SOUTHEAST: *Yano 1984*, *1989⁺*, *1996a⁺*, *b*, *Gradstein & Costa 2003*, *Yano 2006 a⁺*, *b⁺*. BRAZIL WEST-CENTRAL: *Yano 1984*, *1989⁺*, *1996a⁺*, *b*, *Gradstein & Costa 2003*, *Yano 2006 a⁺*, *b⁺*.

SOUTHERN SOUTH AMERICA

Kühnemann 1949[•].

ARGENTINA NORTHEAST: X. ARGENTINA NORTHWEST: X.. ARGENTINA SOUTH: X. CHILE CENTRAL: X. CHILE NORTH: X. CHILE SOUTH: X. DESVENTURADOS IS.: X. JUAN FERNÁNDEZ IS.: *Arnell 1957*. PARAGUAY: X. URUGUAY: *Hässel 1964*.

ANTARCTICA

SUBANTARCTIC ISLANDS

AMSTERDAM–ST. PAUL IS.: *Grolle 2002a*. BOUVET IS.: *Bell & Blom 1986*, *Ochyra & Vána*

1989, *Frisvoll et al. 1995*, *Bednarek-Ochyra et al. 2000*, *Grolle 2002a*. CROZET I.: *Kaalaas 1911*, *Grolle 1972a*, *2002a*. FALKLAND IS.: *Engel 1990*. HEARD–MCDONALD IS.: *Grolle 2002a* [HEARD I.: *Vána & Gremmen 2005*]. KERGUELEN: *Grolle 2002a*, *Vána & Gremmen 2006*. MAQUIRE IS.: X. MARION–PRINCE EDWARD IS.: *Grolle 1971*, *Grolle 2002a*. SOUTH GEORGIA: *Steere 1961b*, *Grolle 1972b*, *Hässel 1977⁺*, *1980⁺*. SOUTH SANDWICH IS.: *Grolle 1972b*, *Ochyra & Vána 1989*, *Bednarek-Ochyra et al. 2000*. TRISTAN DA CUNHA: *Arnell 1958*.

ANTARCTIC CONTINENT

ANTARCTICA: *Steere 1961a*, *Ochyra & Vána 1989*, *Bednarek-Ochyra et al. 2000*.

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Chapter Eleven: *Hamatostrepta concinna* gen. et sp. nov. (Jungermanniopsida, Scapaniaceae), a new Asiatic leafy liverwort from the Sino-Burmese border

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Tamás Pócs

Chapter Thirteen: Bryophytes from the Fiji Islands, IV. The genus *Frullania* Raddi (Jungermanniopsida), I., with description of *F. vivipara* Pócs, spec. nov.

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Abstract

The genus *Hamatostrepta* and its single new species *H. concinna* are described from the Sino-Burmese border region of Asia. The genus is related to *Anastrepta* but differs in its strongly deflexed, deeply trilobed leaves. Ecologically the species grows in alpine liverwort/dwarf shrub heath associated with dwarf *Rhododendrons*.

Introduction

The opportunity for bryologists from the California Academy of Sciences and Royal Botanic Garden Edinburgh to carry out exploration of the remote Gaoligong Shan mountains in

western Yunnan Province of China has been facilitated by the *Biotic Survey of Gaoligong Shan* project (for background information see Chaplin, 2005; Shevock et al., 2006) and has resulted in many noteworthy discoveries of mosses and liverworts. Only at the northern end of this range, in

Fugong and Gongshan counties, are there significant high mountains rising above the tree line to 4000 m and above, and a special effort was made in 2005, 2006, and 2007 to explore parts of these, though access was highly challenging. On the summer 2005 expedition, the Yunnan–Burma (Myanmar) border area of Fugong County proved to be exceptionally rich for bryophytes and the ill-defined border close to the “Yaping Pass” was explored on two occasions. A striking leafy liverwort that was discovered on the border ridge could not be placed in any known genus. It was found in a very small area, which, based on Global Positioning System readings and satellite imagery, appears to be just a few meters inside the Burmese border (B. Bartholomew, pers. comm.). However, in September 2007, on the same ridge further north in Gongshan County, a second colony was discovered, this time well within Yunnan Province. These specimens were subsequently studied at Edinburgh by the authors under the EC SYNTHESYS program, and attempts to identify them with any known genus failed. The taxon is therefore described as a new genus and species below. It is placed in the family Scapaniaceae in the sense of De Roo et al. (2007). The generic name alludes to the deflexed hook-like tips of the leaf lobes, giving the leaves a claw-like appearance; the specific epithet from the neat erect shoots of the plants in the field.

Description

The new genus *Hamatostrepta* and its single new species *Hamatostrepta concinna* are validated by a “descriptio generico-specifica” (Art. 42.1), as follows:

***Hamatostrepta concinna* Váňa & D. G. Long, gen. et sp. nov.** Figures 1, 2.

Anastreptae (Lindb.) Schiffn. affinis sed ramulis omnibus ventrali-intercalaribus, foliis profunde et asymmetrico trilobis lobis in apice longo filiformi terminantibus, basi dorsali decurrenti, margine ventrali folii valde deflexo haud secundo, folii marginibus integris, amphigastriis frequentibus laciniatis caule angustioribus, gemmis nullis differt.

Holotype: Myanmar, Kachin State, Putao District, W slope of Gaoligong Shan (Irrawaddy catchment), Burma–Yunnan border ridge at border marker 31, south of “Yaping Pass,”

27°12'15.4"N, 98°41'39.9"E, exposed rocky W-facing alpine ridge slope, with granite boulders and dwarf *Rhododendrons*, on mossy boulders under dwarf *Rhododendrons*, 3710 m, 16 Aug. 2005, D. G. Long 34854 (E); isotypes: CAS, F, KUN, MO, PE, PRC.

Plants medium-sized to large, 2–6(8) cm long, with leafy shoots 0.8–3.2 mm wide, in loose short turfs, green, olive-green to bronzed or yellowish-brown along the leaf margins; leafy shoots erect, with tips curved towards dorsal side. Branching rare, ventral-intercalary, stolons lacking. Stem rigid, brown to blackish, with the surface smooth, 300–400 µm in diameter, in transverse section with 2–3 layers of outer cells with thick, dark brown walls; inner cells hyaline and slightly larger, with thin walls and somewhat thickened trigones. Rhizoids abundant, relatively short, borne in a more or less continuous line along ventral surface of stem almost to shoot tip, hyaline to slightly brownish. Leaves alternate, succubous, appearing squarrose, convex adaxially, with ventral margin strongly deflexed to deflexed-recurved, dorsal margin also deflexed (giving leaves a “plagiochiloid” appearance), somewhat undulate or crispate (impossible to flatten), asymmetrically trilobed with the dorsal lobe largest, slightly wider than long, 1.35–1.50 mm long and 1.40–1.55 mm wide; leaf margins in places revolute, entire, only in subinvolute leaves some additional teeth present; dorsal margin longer and arcuate, sometimes auriculate, dorsal insertion extending transversely across the stem midline; ventral margin not antically secund, shorter than dorsal margin and almost straight or weakly curved, shortly decurrent on stem. Leaves trilobed to $\frac{1}{3}$ – $\frac{2}{5}$, sinuses obtuse, strongly gibbous; lobes ovate-triangular, long acuminate, mostly ending with filiform uniseriate tip 3–11 cells long, on the ventral base of leaf sometimes with a short cilium with a uniseriate row of isodiametric (not elongate) cells. Upper leaf cells rounded, 25–30 µm diameter, slightly thick-walled, with small trigones, basal cells elongated up to 25×40 µm, with more conspicuous trigones, marginal row of cells with intensively pigmented brown to somewhat reddish cell walls; walls smooth or nearly so. Underleaves small, borne amongst rhizoids, narrower than stem, not connate with leaf base, subulate with 1–2 additional marginal teeth or 2–3-lacinate, at base up to 10 cells wide, mostly with long uniseriate tip, cells of laciniae uniseriate or biseriate at base. Gemmae lacking.

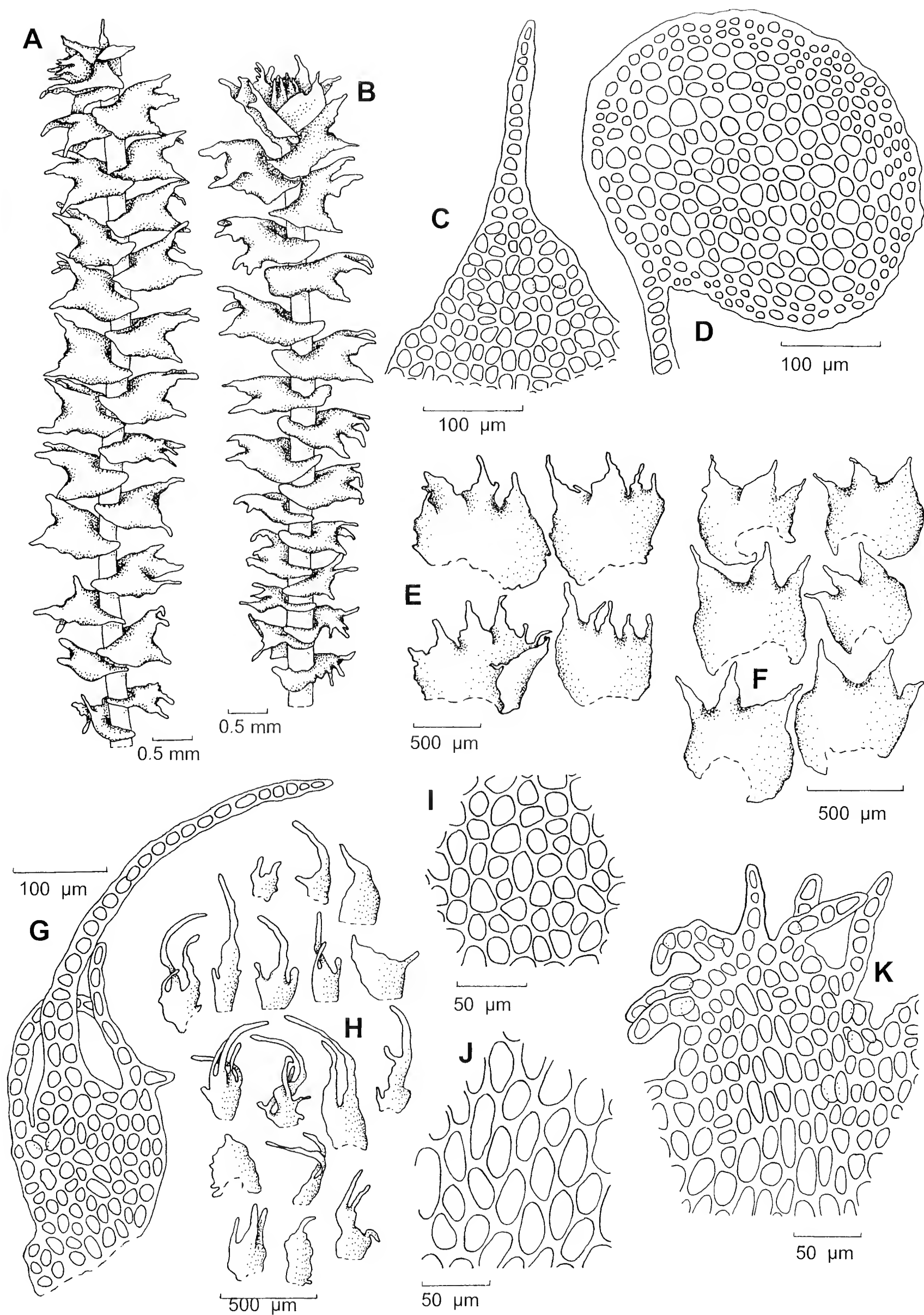


FIG. 1. *Hamatostrepta concinna* Váňa & D.G. Long. (A, B), female shoots with perianth, dorsal view. (C) Leaf lobe apex. (D) Stem transverse section. (E) Female bracts. (F) Leaves. (G, H) Underleaves. (I) Cells from upper part of leaf lamina. (J) Cells from near leaf base. (K) Part of perianth mouth. Drawn from holotype by Daniela Schill.



FIG. 2. *Hamatostrepta concinna* Vána & D. G. Long, dorsal view. Photograph of Long 37252 by Dong Lin.

Dioicous. Androecia intercalary, male bracts in 4–6 pairs, strongly inflated at base, deeply 3-lobed but with several additional marginal teeth; antheridia not seen. Female bracts incised-lacerate, 3–5-lobed, wider than leaves, sometimes with additional teeth on margin. Bracteole deeply bilobed, squarrose, with additional marginal teeth. Perianth terminal, with ventral-intercalary subfloral innovations, ovoid to cylindrical-clavate, in upper part 4–5-plicate, shortly exserted (but immature), 3–6-mm long, 2–3-mm wide; perianth mouth crenulate to shortly ciliate. Sporophyte not present.

Additional Specimen Studied

China, Yunnan Province, Gongshan County, Dulong Xiang, west slope of ridge crest of Gaoli-gong Shan (Irrawaddy catchment), Qi Qi trail at pass to Dulong, 27°41'42.3"N, 98°27'09.9"E, exposed ridge crest with rock outcrops, hollows, and dense *Juniperus/Rhododendron* scrub, on

mossy bank in hollow under dwarf *Rhododendron*, with *Lophozia setosa*, 3700 m, 29 Sept. 2007, D. G. Long & J. Shevock 37252 (paratypes: E, KUN, CAS).

Discussion

Hamatostrepta shows similarities to several genera of the Scapaniaceae, especially those formerly placed in the Lophoziaceae subfamily Lophozioideae by Grolle and Long (2000), but is most closely related to *Anastrepta* on account of the “plagiochiloid” habit of the leaves, which are strongly convex with the dorsal and especially ventral margins conspicuously deflexed. However, it differs strikingly from *Anastrepta* in its lack of lateral-intercalary branches, deeply 3-lobed leaves with filiform lobe apices, the ventral leaf margins which are not dorsally secund, the frequent underleaves, and in the lack of gemmae. In *Anastrepta* (Paton, 1999: fig. 75) the branches are mostly lateral-intercalary, the leaves are very shortly bilobed with acute to rounded lobe apices, the ventral leaf margins though also deflexed are strongly dorsally secund, underleaves are absent or well developed only near female inflorescences, and the leaves are often gemmiferous.

Asymmetrically trilobed leaves are also present in *Chandonanthus*, *Tritomaria*, and in some species of *Barbilophozia* and *Lophozia*. All four genera mentioned have a very different leaf insertion (transverse to oblique, ventral part not deflexed) and leaves are usually concave rather than convex. Only exceptionally can leaves be slightly convex, as in a few *Barbilophozia* and *Lophozia* species. *Chandonanthus* s.s. differs in its terminal branching, deeply 2–4-lobed plicate-undulate leaves with marginal teeth, very large underleaves (about half size of leaves), and bulging trigones of leaf-cells (Schuster, 2002). In *Tritomaria* branching is terminal and lateral-intercalary, leaves are not convex, underleaves are absent, and gemmae present (Paton, 1999).

The southern hemisphere genus *Nothostrepta* shows some similarities; in the past it has been treated as part of *Anastrepta* but is now considered to belong to the separate subfamily Jamesonielloideae of Lophoziaceae (Schuster, 2002) or even a separate family, Jamesoniellaceae (He-Nygrén et al., 2006). *Nothostrepta* differs from both *Anastrepta* and *Hamatostrepta* in its shoot tips which are deflexed downwards not upwards, its

underleaves which are large and connate with leaf bases on one side, rhizoids in fascicles originating from ventral leaf bases, its dorsal leaf insertion which is interlocking, its strongly verrucose-striolate surface features, and in its long cylindric perianths (Schuster, 2002).

The close relationship of *Hamatostrepta* to *Anastrepta* is supported by preliminary molecular data. On the basis of a sequence of the chloroplast region *trnL*, *Hamatostrepta* nested as a sister taxon to *Anastrepta orcadensis* in a clade otherwise containing several species of *Anastrophyllum* (corresponding with De Roo et al., 2007). However, a full molecular evaluation using several additional markers is desirable. The genus *Barbilophozia* has only recently been reported for the first time from Yunnan (Wu & Wang, 2000) under the name *Barbilophozia hatcheri* (A. Evans) Loeske. The illustration of this collection (loc. cit., fig. 17.1–17.5, from Dulongjiang, Gongshan County, 2000 m alt., *M.-Z. Wang 11567c*) shows a plant similar to *Hamatostrepta* in its asymmetrically 3-lobed leaves but with obtuse not filiform lobe apices; no underleaves are illustrated.

Ecology

The habitat of *Hamatostrepta* is typical of many of the larger leafy liverworts found in the Sino-Himalayan region in alpine liverwort/dwarf shrub heath communities. The type locality was on an exposed rocky west-facing alpine ridge slope at 3710 m, with granite boulders and dwarf *Rhododendrons*, where it grew on mossy boulders under dwarf *Rhododendrons*, intermixed in loose turf with *Anastrophyllum alpinum* Steph., *A. donnianum* (Hook.) Steph., *Anastrepta orcadensis* (Hook.) Schiffn., *Dicranum* sp., *Hypnum* sp., *Plagiochila* sp., *Polytrichastrum xanthopilum* (Mitt.) G. L. Sm. Merr., and *Scapania secunda* Steph. On the adjacent boulders *Apomarsupella revoluta* (Nees) R.M.Schust., *Bazzania pearsonii* Steph., *B. tricrenata* (Wahlenb.) Lindb., *Horikawaella subacuta* (Herzog) S. Hatt. & Amak., *Mylia taylorii* (Hook.) Gray, *Paraleucobryum enerve* (Thed.) Loeske, *Racomitrium joseph-hookeri* Frisvoll, *Takakia ceratophylla* (Mitt.) Grolle, and *Tetraplodon mnioides* (Hedw.) Bruch et al. were growing. The plant was recognized as potentially a new genus in the field, and an extensive search of the immediate vicinity was made but only a very small highly localized colony was found.

Similar habitats in Gongshan County were searched in 2006 without success, but in 2007 a second colony was discovered some 80 km north of the first locality. The elevation and habitat were almost identical to those at the first locality, the dominant associates being the leafy liverworts *Anastrophyllum alpinum* Steph. and *Lophozia setosa* (Mitt.) Steph., along with *Anastrepta orcadensis* (Hook.) Schiffn., *Herbertus dicranus* (Taylor ex Gottsche et al.) Trevis., *Plagiochila semidecurrens* (Lehm. & Lindenb.) Lindenb., and *Scapania ferruginea* (Lehm. & Lindenb.) Gottsche et al.

However, the rugged and inaccessible nature of this habitat along the border of Myanmar and Yunnan make it likely that additional populations could exist in similar habitats in other places along the ridge. At least on the Chinese side, the area is identified for long-term conservation as part of the Gaoligongshan Nature Reserve.

Acknowledgments

This study was performed at the Royal Botanic Garden Edinburgh under the EC SYNTHESYS exchange program; J.V. also acknowledges financial support at Charles University from the MSM project 0021620828. D.G.L. wishes to acknowledge support for field work in China on the *Biotic Survey of Gaoligong Shan* project by the U.S. National Science Foundation grant DEB-0103795. Excellent logistical support for this field work was provided by the Kunming Institute of Botany, especially Professor Li Heng, Dao Zhiling, and Dr. Ji Yunheng, and the California Academy of Sciences, especially Dr. Peter Fritsch, Dr. Bruce Bartholomew, and Dr. David Kavanaugh. Dr. Robert Mill (Edinburgh) is thanked for preparing the Latin diagnosis, Daniela Schill (Edinburgh) for drawing Figure 1, and Dong Lin (San Francisco) for Figure 2. Bruce Bartholomew is also thanked for supplying geographical information, Laura Forrest for providing a *trnL* sequence of *Hamatostrepta*, and Jim Shevock for helpful comments on the manuscript.

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FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Six: Liverwort Floristics and Revisions—Asia and Australasia

Chapter Twelve: Bryophytes from the Fiji Islands, III. The genus *Phaeolejeunea* Mizut. (Lejeuneaceae), with detailed description of *P. amicorum* (Hürl.) Pócs, stat. nov.

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Abstract

The genus *Phaeolejeunea* is new to the Fiji Islands, represented by one species previously known only from 'Eua (Tonga Islands) under the name *Phaeolejeunea etesseana* Mizut. ssp. *amicorum* Hürl. As a result of a study of all species of the genus, this taxon proved sufficiently distinct as to warrant recognition at the rank of species. It is endemic to the Fiji and Tonga islands, at the border of Eastern Melanesia and Western Polynesia in the Southern Pacific. First observations on the oil-bodies of *Phaeolejeunea* are given.

Introduction

Phaeolejeunea Mizut. (1968) is a well-defined Indomalesian–Pacific genus of the Lejeuneaceae, characterized by its lobule with 2–3 large teeth, one of which bears on its inner side a postically reflexed, elongated structure with the entally displaced hyaline papilla at its apex. The genus is

also characterized by its isodiametric leaf cells without blackish pigmentation, thick-walled stem cells, *Frullania*-type branching, and very broad reniform underleaves, flattened, 4-winged perianth with (1–)2 innovations (Mizutani, 1968; Gradstein et al., 2002). The taxonomic position of the genus was clarified by molecular and morphological analysis based on our Fijian specimen, and

the genus proved to be a neighbor of *Lopholejeunea* group within the Ptychanthoideae subfamily (Wilson et al., 2006).

Hürlimann (1991) described *Phaeolejeunea etesseana* Mizut. ssp. *amicorum* Hürl. from the small 'Eua Island in Tonga Archipelago. I collected the same plant at several localities in the Fijian Islands with my wife in September 2003. Comparison of these samples with other species of *Phaeolejeunea* revealed that the taxon described from Tonga and recently found on Fiji Islands differs from *Phaeolejeunea etesseana* (Steph.) Mizut. at the species level, as will be discussed below. *Phaeolejeunea etesseana*, described from New Caledonia, is the only species of the genus with elongated lobule 1.5–2× as long as wide. The other species have more or less round or triangular lobules. In this respect the Fijian and Tongan plants are similar to *Phaeolejeunea latistipula* (Schiffn.) Mizut., but differ from all other species by their flat, rather than saccately involuted lobule with only slightly arcuate sinus (as already mentioned by Hürlimann, 1991). In the following, I give a detailed description of the Fijian plant, including the description of oil-bodies, which supports and supplements the short account and drawing given by Hürlimann (1991).

Taxonomic Treatment

Phaeolejeunea amicum (Hürl.) Pócs, stat. nov.
Figures 1, 2a–e, 3a–c.

Phaeolejeunea etesseana (Steph.) Mizut. ssp.
amicorum Hürlimann, 1991, *Bauhinia* 9/4:
263.

Olive-green, corticolous plant with sparsely branched shoots up to 4–6(–8) cm length and up to 2.3 mm width. Stem rigid, pale green to brown, 150–220 µm diam., in which 20–28 medullary cells with strongly thickened walls are surrounded by 40–45 somewhat larger cortical cells with often brown-pigmented, less thickened walls. Ventral merophyte 7–10 cells wide. Branching *Frullania*-type. Rhizoids reddish brown, fasciculate. Leaves flat, more or less adherent to the substrate, falcato-ovate, 1.5–1.75 mm long and 1.5 mm wide. Lobe cells pentagonal-hexagonal isodiametric, 24–30 µm diam., with narrow trigones and otherwise evenly thickened walls, except that along the wall edges the median regions of the

walls remain unthickened (see Fig. 2d). Lobule ovate-triangular, only slightly longer than wide, flat, not involute, with almost straight keel and usually bearing 2–3 triangular, 100–200-µm-long teeth, and a narrow appendage adherent to the inner side of the apical (usually second) tooth that is 1 cell wide and 2–3 cells long, with the hyaline papilla at its apex. Lobule cells 15–25 µm, slightly elongated, with bulging trigones and intermediate cell wall thickenings. Underleaves reniform, transverse obovate (never truncate), contiguous or distant (never imbricate), 0.5–0.53 mm long and 1.2–1.4 mm wide with flat margin and with U-shaped insertion. All known specimens sterile except for one male. Oil-bodies (first observation for the genus): 9–25, *Bazzania* type (Fig. 2e).

SPECIMENS EXAMINED—New to **Fiji Islands, Taveuni I.**: Central part of the island. Along the road from Wairiki to Des Voeux Peak, on the NW slopes, at 715–750 m alt., 16°49.831–915'S, 179°58.643–731'W, ramicolous in low canopy mossy montane rain forest with transitions to elfin forest, S. & T. Pócs 03289/L (EGR). **Kadavu (Kandavu) I.**: Central part, 3 km NNE of Vunisea, at 140 m alt., 19°01.83–92'S, 178°10.77–81'E, corticolous in mesic evergreen forest, S. & T. Pócs 03301/AT (EGR). Central part, on the coastal ridge, 0.5–1.5 km N of Vunisea, at 40–80 m alt., 19°02.390–529'S, 178°09.554–608'E. On *Gymnostoma vitiense* (Casuarinaceae) bark in dry evergreen microphyllous forest with emergent trees, many creeping *Flagellaria*, and with *Schizaea dichotoma* and Cyperaceae in the ground layer, S. & T. Pócs 03303/B (EGR, SUVA). Western part, 2 km NE of Tavuki village, at 170–200 m alt., 19°03.829–04.102'S, 178°07.771–921'E. On *Gymnostoma* bark in dry evergreen microphyllous forest, S. & T. Pócs 03304/L, 03309/AC (EGR, FMNH, SUVA). Central part, on the ridge SE of Vunisea telecom tower at 100–120 m alt., 19°03.214–300'S, 178°09.836–877'E. On *Gymnostoma* bark in dry evergreen microphyllous forest, S. & T. Pócs 03307/F (EGR, SUVA). Western part, 3 km ENE of Tavuki village, in a rocky streambed above waterfalls, at 120 m alt., 19°04.354'S, 178°08.700'E. Corticolous in a riverine forest with tree ferns and many buttressed trees on big boulders, S. & T. Pócs 03310/A (EGR, FMNH, GOET).

KNOWN DISTRIBUTION (Hürlimann, 1991)—**Tonga Islands, 'Eua I.**: mit anderen Lejeuneaceen auf Rinde eines Baums in mesophilem Primärwald, am Weg von Fuai zum Eastern Ridge, ca. 130 m, H. Hürlimann T 837, 1951 (holotype: z, isotype: G).

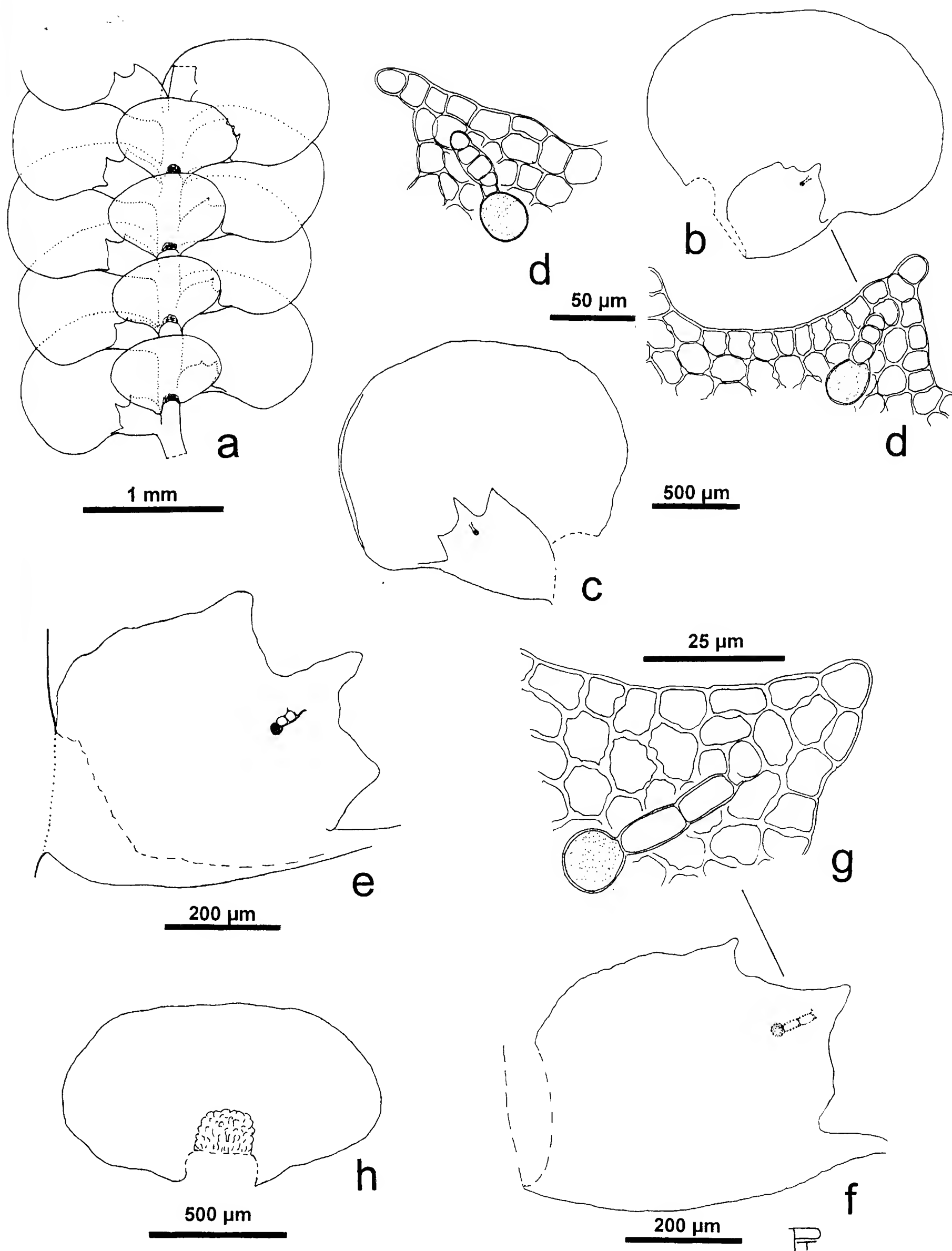


FIG. 1. *Phaeolejeunea amicorum* (Hürl.) Pócs. (a) Habit, ventral view. (b, c) Leaves. (d, g) Lobule teeth with entally displaced hyaline papilla on a filamentous stalk. (e, f) Lobules. (h) Underleaf. (Parts a–e are drawn from *Pócs* 03304/L and f–h from *Pócs* 03289/L.)

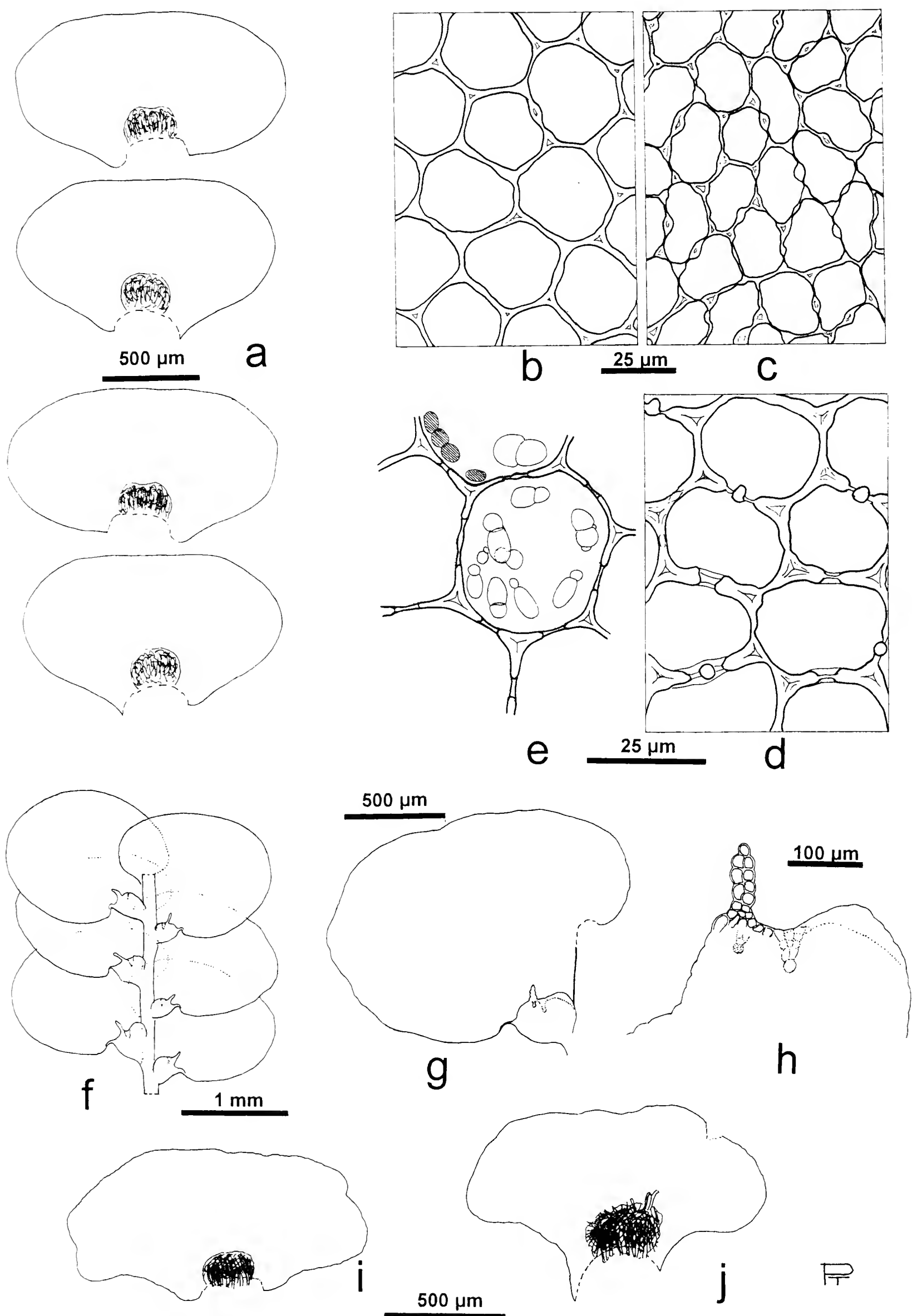


FIG. 2. **a–e.** *Phaeolejeunea amicorum* (Hürl.) Pócs. (**a**) Underleaves. (**b, d**) Lobe cells. (**c**) Lobule cells. (**e**) Oil-bodies in lobe cells. **f–j.** *Phaeolejeunea latistipula* (Schiffn.) Mizut. (**f**) Habit, ventral view after underleaves removed. (**g**) Leaf. (**h**) Lobule teeth. (**i, j**) Underleaves. (Parts **a–d** are drawn from Pócs 03304/L, **e** from Pócs 03301/AT, **f–h** from Norris & Roberts 48789).

Other Species Examined

Phaeolejeunea etesseana (Steph.) Mizut. Figure 3d.

SPECIMENS EXAMINED—**Nouvelle Calédonie**: A la face supérieure d'un tronc ascendant en forêt hygrophile primaire, pente Sud de la baie de Kouébuni vis-a-vis de la maison Tanguy, 40 m, *H. Hiirlimann* 2260 *a* (GOET). Sur l'écorce d'un arbre, forêt hygrophile au Mé Aoui, 500 m, *Guillaumin et Baumann* 10510 (GOET).

KNOWN DISTRIBUTION—(Mizutani, 1968; Hiirlimann, 1991)—New Caledonia and Loyalty Islands 100 km eastwards.

Phaeolejeunea latistipula (Schiffn.) Mizut. Figure 2f–j.

SPECIMENS EXAMINED—**Solomon Islands, San Cristobal I.**: Open parkland on coast near Kira-Kira village at sea level, corticolous, *Norris & Roberts* 487889 (H, Pócs et al., 1995).

KNOWN DISTRIBUTION (Mizutani, 1968; Gradstein et al., 2002)—Java, Philippines, Taiwan, Mariana Islands, Caroline Islands, West Irian, Papua New Guinea, Bismarck Archip.: Anchorete I. and New Hanover (Lavongai) I., Solomon Islands.

Discussion

The differences between the three species are quite clear cut. *Phaeolejeunea etesseana* is well characterized by the involute lobule, which even

in open form is 1.5–2× longer than wide, and its teeth are obtuse. *Phaeolejeunea latistipula* has a quite complex lobule with a very narrow and acute first lobule tooth with an appendage more than one cell wide and very large underleaves. *Phaeolejeunea amicorum* is distinct in its flat lobe and lobule without involute margins, by its almost straight keel with shallow sinus and by its smaller size, by its transverse obovate (never truncate) underleaves, and by its habit of growing appressed to the substrate. There is a fourth species of *Phaeolejeunea* described as *P. inermis* (Steph.) Mizut. and known only from its type locality in Papua New Guinea. Already Mizutani (1968) presumes it to be a poorly developed form of *P. latistipula*. Indeed, such depauperate forms occur within all the three other species, wherein the number of lobule teeth are reduced. The specific characters are summarized in Table 1.

A quite unique feature in all the three species of the genus is the triangular or linear appendage. Mizutani (1968) interprets this structure as the entally disposed second tooth, with a hyaline papilla at its apex. As it seldom appears on the lobule margin and is often shifted to the inner surface of the longest tooth, it is an interesting derived character known only in this genus within the family Lejeuneaceae. Its shape varies between species: triangular and more than one cell wide in *P. latistipula*, while short filamentous and consisting of only one cell row in *P. amicorum* and in *P. etesseana*. The position of lobule teeth are variable, one of them turning inside in *P. etesseana* and in *P. latistipula*, while all are straight and in the plane of the lobule in *P. amicorum*.

TABLE 1. The comparative properties of the known *Phycolejeunea* species (bold setting emphasizes specific characters).

	<i>P. amicorum</i>	<i>P. etesseana</i>	<i>P. inermis</i>	<i>P. latistipula</i>
Shoot width (mm)	1.8–2.3	3	1.2	2.5–3
Leaf length (mm)	1.5–1.75	1.25–1.7	0.6–0.75	1.2–1.6
Lobe apex	flat	usually strongly involute	flat	flat or involute
Lobule	ovate, almost as long as wide, flat	elongate, 1.5–2 longer than wide, saccate	elongate-ovate, saccate	ovate-triangular, saccate
Lobule margin	flat	usually strongly inflated	inflated	usually inflated
Normal lobule teeth	2–3, triangular	1–3, wide triangular	1, acute triangular	2–3, acute
Appendage (modified 2nd tooth)	filamentous, row of 2 (3) cells	short filamentous, row of 2 cells	?	triangular, with 2–4 cellular basis
Keel angle to lobe	flat	sharp	wide	sharp
Underleaf position	contiguous to distant	imbricate	imbricate	imbricate
Underleaf/stem width ratio	4–6×	3–4×	5–7×	5–6×
Underleaf apex	round	often truncate	round	truncate
Rhizoid color	reddish brown	pale or dull brown	?	reddish brown

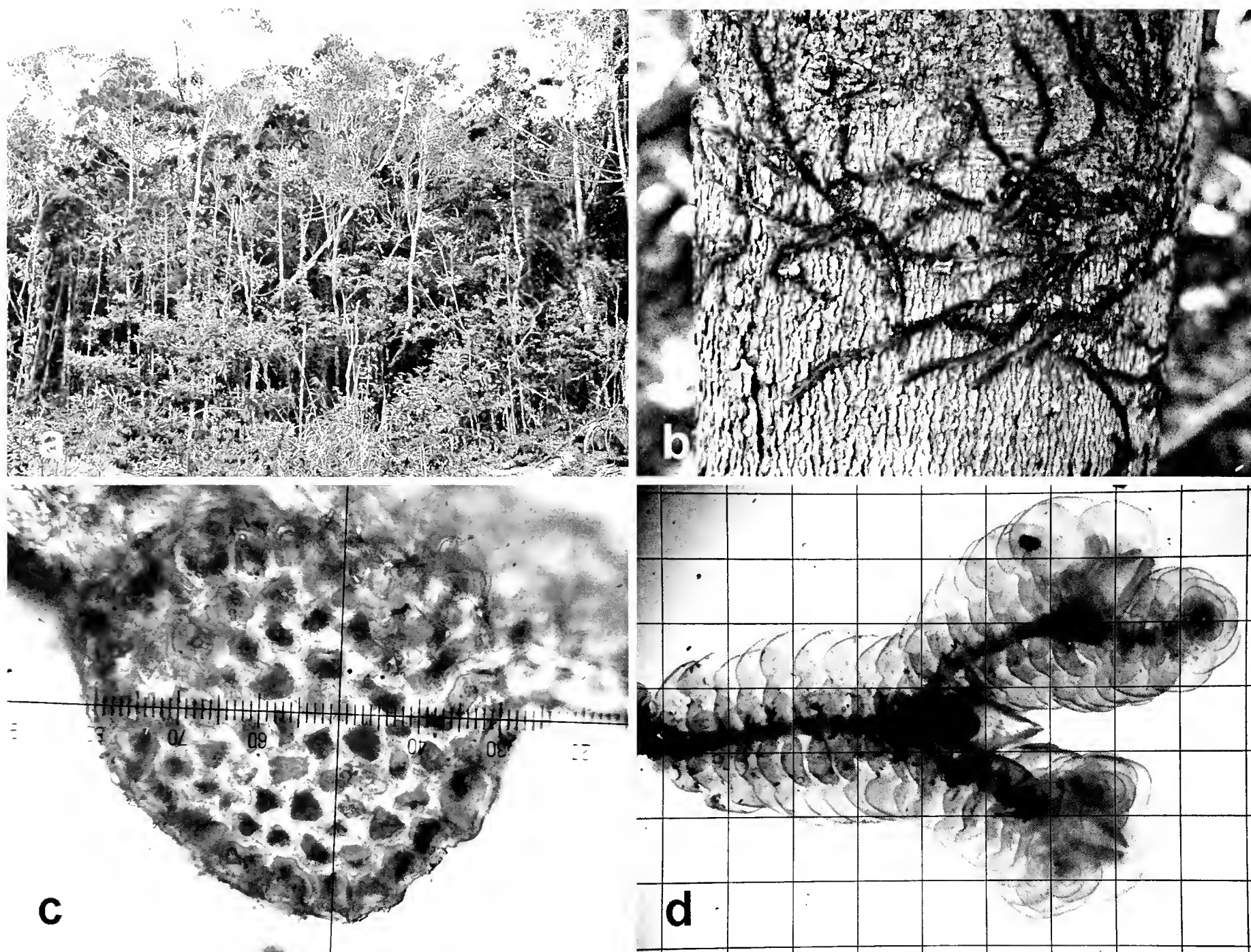


FIG. 3. (a) Microphyllous dry evergreen forest with *Gymnostoma vitiensis* L. A. S. Johnson (Casuarinaceae) trees (dark foliage) near Vunisea telecom tower (locality 03307). (b) *Phaeolejeunea amicorum* (Hürl.) Pócs creeping on *Gymnostoma* bark (Pócs 03307/F). (c) Stem cross section of *Phaeolejeunea amicorum* (Pócs 03307/F, grid = 4 µm). (d) Habit, ventral view of *Phaeolejeunea etesseana* (Steph.) Mizut. (Gulleaumin & Baumann 10510, grid = 1 mm).

Concerning the ecology of the *Phaeolejeunea* species, they all seem to be typically corticolous and at least *P. amicorum* prefers rather open, drier habitats. The other two species seem to occur in rain forests. Their altitudinal distribution extends from the sea level to at least 1000 m.

The distributions of these three species are interesting. While *P. latistipula* is a widespread Malesian–Oceanian species, the two other species (and *P. inermis* if we accept it as a species) are distributed in relatively small areas. *P. amicorum* is restricted to the Tonga and Fiji islands, *P. etesseana* to New Caledonia and the neighboring Loyalty Islands, and finally *P. inermis* to Papua New Guinea. It is an interesting fact that *P. amicorum* is known only from the oldest island in the Tonga Archipelago. 'Eua is thought to be partly composed of an ancient fragment of Gondwana, where it broke off from Norfolk Ridge near New

Caledonia about 40 million years ago. Then it has moved eastward, coming into close contact with Fiji (5 million years ago) and finally moved to Tonga (Mueller-Dombois & Fosberg, 1998).

Phaeolejeunea amicorum in the Fiji Islands was collected almost solely from the small island of Kadavu. Kadavu is a late Cenozoic (Pliocene) volcanic island (Terry, 2002) with vegetation quite different from the rest of Fiji Islands, being dominated by open, temporarily dry and semidry *Gymnostoma vitiense* (Casuarinaceae) forests (Fig. 3a), in spite of the humid tropical climate, on orange-colored or lilac regolith soils developed from probably ultrabasic bedrocks. On the bark of *Gymnostoma vitiense* trees, a rich, relatively xerotolerant epiphytic liverwort vegetation developed, including many *Frullania* and Lejeuneaceae species, with the dominance of *P. amicorum* (Fig. 3b).

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The author is indebted to his wife, Sarolta (Saci) Pócs, for her participating in the collection and preparation of specimens and to Prof. S. Rob Gradstein, to Matt Renner, and to Matt von Konrat for their very useful advice. The financial support of AMFK (Hungarian Ministry of Education) and by ALCOA Foundations (USA) is gratefully acknowledged.

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FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Six: Liverwort Floristics and Revisions—Asia and Australasia

Chapter Thirteen: Bryophytes from the Fiji Islands, IV. The genus *Frullania* Raddi (Jungermanniopsida), I., with description of *F. vivipara* Pócs, spec. nov.

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Abstract

The genus *Frullania* was previously known to be represented in the Fiji Islands by 20 species. From recent collections, 17 species were identified, of which five species proved to be new to the islands: *Frullania angulistipa*, *Frullania baladina*, *Frullania chevalieri*, *Frullania ericoides*, and *Frullania gracilis*. One other, *Frullania vivipara*, is described as new to science. The enumeration is followed by a phytogeographic evaluation.

Introduction

The historical bryophyte collections made by Seemann from Fiji Islands in 1860 were studied by Mitten (1862), who, among others, described *Frullania deflexa* Mitt., *F. meteoroides* Mitt. (= *F. serrata* Gottsche et al.), *F. trichodes* Mitt. (Mitten,

1862), and *F. vaga* Mitt. (Mitten in Seemann, 1865–1873). He also recorded *F. nodulosa* (Reinw. et al.) Nees in Gottsche et al. and *F. pacifica* Taylor (syn. of *F. apiculata* f. *aculeata* Verd.) and, from Graeffe's collection made in 1864, described *F. angulosa* Mitt. (= *F. intermedia* var. *non-apiculata* S. Hatt.) (Mitten in Seemann,

1865–1873). Jack and Stephani (1894) described *F. ampullacea* Jack. & Steph. and *F. curvirostris* Jack. & Steph. (= *F. novocurvirostris* S. Hatt., 1981, nom. nov.). Interestingly, Verdoorn's revision on the Pacific Frullaniaceae does not mention any new records from Fiji Islands, although *F. graeffeana* Steph. was synonymized with *F. intermedia* (Nees in Reinw. et al.) Dumort. (Verdoorn, 1928, 1930b). Later, a number of Fijian species were studied by Hattori (1980a, 1981) during his thorough revisions of Asian–Australasian–Oceanian *Frullania*. He also described *F. auriculata* S. Hatt. and *F. epiphylla* S. Hatt. ssp. *fijiensis* S. Hatt. and *F. intermedia* var. *non-apiculata* S. Hatt., and communicated *F. capillaris* Steph., *F. immersa* Steph. from the collection of Iwatsuki and Kitagawa (Hattori, 1985). Finally, Schuster discovered and described *Neohattoria parhamii* R. M. Schust.—now *Frullania parhamii* (R.M. Schust.) R. M. Schust.—from Vanua Levu Island of Fiji (Schuster, 1963). Based on some other publications in the *Prodromus* of Miller et al. (1983), *F. hamata* Steph., *F. gaudichaudii* (Nees et Mont.) Nees et Mont., *F. hypoleuca* Nees, and *F. neurota* Taylor also occur. Altogether, hitherto 20 species were known from the Fiji Islands.

During August–September 2003, the author with his wife collected more than 60 specimens of *Frullania* on Viti Levu, Taveuni, and Kadavu (Kandavu) islands. The greater part of them were identified by the author, and records of five species proved to be new for Fiji Islands and one new to science. In addition, Jens Eggers (Schenefeld, Germany) collected a further two *Frullania* specimens in 1999, of which one appears to be a new record but with the identity unknown. Finally, the new records contribute to our existing knowledge of *Frullania* and a brief examination of phytogeographic patterns in the region is provided.

The collected specimens are deposited in the Herbarium of Eger College (EGR), and their duplicates, when available, in the Herbarium of the University of the South Pacific (SUVA) and in the Field Museum, Chicago (F).

Taxonomy

Frullania is a large and complex genus and has been variously divided into subgenera (von Konrat & Braggins, 2001). The subgeneric

classification scheme here largely follows Schuster (1992), with modification from Hattori (1984, 1986).

Subgenus *AUSTRALES* (Verd.) S. Hatt.

Frullania baladina Gottsche ex Steph. Illustration: see Hattori, 1984: 406, fig. 1.

MATERIAL EXAMINED—**Viti Levu I.:** Southern coast (“Coral Coast”) in the high rainfall area. Pacific Harbour township area, at 2–3 m alt. On garden and on roadside trees. S. & T. Pócs 03259/N. **Kadavu** (Kandavu) **I.:** Western part, 3 km NNE of Tavuki village, on a ridge at 220–240 m alt. Corticolous in dry evergreen microphyllous *Gymnostoma vitiense* L.A.S. Johnson (Casuarinaceae; syn.: *Casuarina nodiflora* Forst. f.) forest. S. & T. Pócs 03305/S.

DISTRIBUTION—New to Fiji, it was previously considered to be a New Caledonian endemic (Hattori, 1984). It is very close to or identical with *F. campanulata* Sande Lac. from Java and Sumatra and with *F. cataractarum* Steph. from New South Wales, Australia. If this can be proved, then the Fijian locality is the easternmost occurrence of a Malesian–Pacific species and of the subgenus.

Subgenus *DIASLOBA* Spruce

Frullania gracilis (Reinw. et al.) Dumort. Illustration: Hattori, 1976a: 10, fig. 171; 1980b: 106, fig. 228h–o.

MATERIAL EXAMINED—**Taveuni I.:** Central part of the island. Along the road from Wairiki to Des Voeux Peak, on the NW slopes at 600–750 m. On bark and on canopy branches in montane rain forest rich in epiphytes. S. & T. Pócs 03288/AQ, 02289/B.

DISTRIBUTION—New to Fiji Islands. Widespread Indomalaysian–Pacific species distributed from India to the Caroline Islands.

Subgenus *FRULLANIA* Raddi

Frullania apiculata (Reinw. et al.) Dumort. Illustration: Hattori, 1980b: 106, fig. 228a–g.

MATERIAL EXAMINED—**Taveuni I.:** NE side of Des Voeux Peak, at 1040–1150 m alt. Corticolous in a 4–8 m high mossy elfin forest, very rich in epiphytes. S. & T. Pócs 03279/K. **Kadavu I.:** Western part, 2 km NE of Tavuki village, 150–200 m, on decaying wood and on bark in dry evergreen *Gymnostoma vitiense* forest. S. & T. Pócs 03304/C, E, F; 03309/AJ.

DISTRIBUTION—Widespread Palaeotropical species, distributed from West Africa to Hawaii.

Frullania ternatensis Gottsche in Gottsche et al.
Illustration: Hattori, 1973: 81–83, figs. 40–42.

MATERIAL EXAMINED—**Viti Levu I.:** Central part, NE edge of Rairaimatuku Plateau, above Naqelewai village, S from “Barclay’s Point,” at 855–945 m alt. Corticolous and hanging epiphyte in montane mossy (cloud) forest. *S. & T. Pócs 03273/A, D.* On the ridge of Rairaimatuku Plateau 10 km SSE of Navai. Mossy elfin forest (cloud forest) built up mostly by *Cyathea* sp. and by the 3–4 m high *Alpinia boia*, at 990–1010 m alt. On tree fern stem. *S. & T. Pócs 03274/B.* **Taveuni I.:** Central part, Des Voeux Peak at 1180–1194 m alt. On bark and twigs in a 1.5–2.5 m high bush formed by a pachycaul Asteraceae on the summit ridge. *S. & T. Pócs 03278/E, F.* NE slope of Des Voeux Peak, at 960 m alt. On the bark of fallen canopy branches in a 10–20 m high, mossy montane rain forest. *S. & T. Pócs 03280/V.*

DISTRIBUTION—Widespread Indomalesian–Australasian species, from Ceylon to Fiji.

Frullania trichodes Mitt. Illustrations: Verdoorn, 1930: 123–124, figs. 194–196; Hattori, 1974a: 187, fig. 86 under *F. vethii* Sande Lac.

MATERIAL EXAMINED—**Viti Levu I.:** Central part, NE edge of Rairaimatuku Plateau, above Naquelevai village, 855–945 m alt. Epiphyllous and on the pseudostem of *Alpinia boia* (Zingiberaceae). *S. & T. Pócs 03273/BA.* **Kadavu I.:** Central part, on the ridge SE of Vunisea telecom tower at 100–120 m alt. Corticolous in dry evergreen microphyllous forest with emergent *Gymnostoma vitiense* trees, on lilac volcanic soil. *S. & T. Pócs 03307/A.* Western part of the island, 2 km NE of Tavuki village, at 150–200 m alt. Corticolous in dry evergreen microphyllous forest *S. & T. Pócs 03304/H, T; 03309/A.*

DISTRIBUTION—Widely distributed Indomalesian–Pacific species.

SUBGENUS *FUSIORIELLIGERAE* (Verd.) S. Hatt.

Frullania gaudichaudii (Nees et Mont.) Nees et Mont. Illustration: Hattori, 1972: 124–127, figs. 10–13; 1975: 143, fig. 159.

MATERIAL EXAMINED—**Taveuni I.:** E side of the island, around the 1st Tavoro Waterfalls, above Korovou (Bouma) village, at 10–100 m alt. Corticolous in very wet lowland rain forest and in woody cultivation, with many tree ferns and epiphytes. *S. & T. Pócs 03282/W.* Central part of the island. Along the road from Wairiki to Des Voeux Peak, on the NW slopes, at 600–700 m alt.

On tree fern stem in montane rainforest rich in epiphytes. *S. & T. Pócs 03288/H.* **Kadavu I.:** Central part, 2–3 km NNE of Vunisea, along the Namara Road, in a valley below waterfall, at 110–150 m alt. Corticolous, covered by epiphylls in a less disturbed lowland rain forest along rocky streamlet. *S. & T. Pócs 03301/W.*

DISTRIBUTION—Indomalayan–Pacific species also occurring in South America (Guiana, Brazil).

Subgenus *HOMOTROPANTHA* Spruce

Frullania deflexa Mitt. Illustration: Hattori, 1980a: 227, fig. 38.

MATERIAL EXAMINED—**Viti Levu I.:** Central part, below the NE escarpment of Rairaimatuku Plateau, in Naquelevai village, at 210–220 m alt. On bark of orchard trees in cultivated area. *S. & T. Pócs 03270/A.*

DISTRIBUTION—East Melanesian endemic known from New Caledonia, Vanuatu, Fiji, and Samoa (Hattori, 1980a).

Frullania intermedia (Reinw. et al.) Dumort. Illustration: Hattori, 1980a: 187, fig. 13; 189, fig. 14.

MATERIAL EXAMINED—**Taveuni I.:** NE part, on the ridge between Qeleni and Welagi villages, at 500 m alt. Submontane rain forest with many tree ferns along brook. *S. & T. Pócs 03281/L.* Central part. Along the road from Wairiki to Des Voeux Peak, on the NW slopes at 600–750 m. Ramicolous in montane rain forest. *S. & T. Pócs 03288/A.*

DISTRIBUTION—Indomalesian–Pacific species distributed from Ceylon to Samoa.

Frullania intermedia (Reinw. et al.) Dumort. **var. non-apiculata** S. Hatt. Illustration: Hattori, 1975: 192, fig. 15.

MATERIAL EXAMINED—**Taveuni I.:** Together with the second specimen above, *S. & T. Pócs 03288/BJ, 03289/AS.*

DISTRIBUTION—Fiji, Samoa, Philippines. A taxon of doubtful rank. Mitten (1871) described and Verdoorn (1930a) recognized it at the species level, as *F. angulosa*. Hattori first considered it at the varietal level (Hattori, 1975) as *F. intermedia* var. *non-apiculata*. Later (Hattori, 1980a) himself synonymized it with the typical *F. intermedia*, which seems to be the correct solution, being probably only an environmental modification. However, we have provisionally maintained recognition at a varietal level, until further

examinations, as it seems to be restricted to a smaller area within the distribution of the typical variety.

Frullania nodulosa (Reinw. et al.) Nees in Gottsche et al. Illustrations: Hattori, 1980a: 209, fig. 28; 212, fig. 29.

Synonymy is provided by Verdoorn (1930a: 177) and Kamimura (1961: 57), excluding *F. brotheri* Steph., which Hattori (1980a: 222–224) recognized as a distinct species.

MATERIAL EXAMINED—**Viti Levu I.**: Central part, below the NE escarpment of Rairamatuku Plateau, 1 km NW of Naquelewai village, in the Naboubuco River valley, at 250 m alt. Corticolous in a wet lowland rain forest rich in epiphylls. *S. & T. Pócs 03271/B*. Southern coast (“Coral Coast”) in the high rainfall area. Pacific Harbour township area, at 2–3 m alt. On garden and on roadside trees. *S. & T. Pócs 03259/AO*. Southern coast between Navula and Lombau villages, along the Queens Road, at 2–3 m alt. Corticolous in a 10–12 m high *Pandanus tectorius*-dominated swamp forest adjoining mangroves along lagoons. *S. & T. Pócs 03260/J*. Near Nabukavesi village, 10 km N of Lombau, at 30–60 m alt. Primary, wet lowland rain forest, on rugged volcanic hills, partly along streamlet. *S. & T. Pócs 03261/A*. ESE part, Colo-i-Suva Forest Park, along streamlet, corticolous, 200 m alt. *J. Eggers FID 1/4*.

DISTRIBUTION—Pantropical (lowland rain forest).

Subgenus *MICROFRULLANIA* R.M. Schust.

Frullania chevalieri (R.M. Schust.) R.M. Schust. Illustrations: Schuster, 1970: 291, fig. 5.6–5.11 under *Neohattoria chevalieri* R. M. Schust. Hattori, 1976b: 80, fig. 1 under *Schusterella chevalieri* (R.M. Schust.) S. Hatt. von Konrat et al., 2006: 146, fig. 2; 148–149: figs. 3a–e, 4a.

MATERIAL EXAMINED—**Taveuni I.**: Central part of the island. Des Voeux Peak. Ramicolous in a 1.5–2.5 m high bush formed by a pachycaul Asteraceae on the summit ridge, at 1180–1194 m alt. *S. & T. Pócs 03278/G*. Det. M. von Konrat.

DISTRIBUTION—New to Fiji Islands. This peculiar species was described by Schuster (1970) from New Caledonia as *Neohattoria*, where it has been since repeatedly collected (Hattori, 1984) and its taxonomic position was changed (Hattori et al., 1972; Schuster, 1992). It was also recently discovered in New Zealand (von Konrat et al., 2006). Von Konrat et al. (2006) also provided

phytochemical and morphological evidence confirming its relationship with *Frullania*. Its discovery in the Fiji Islands provides strong support suggesting that the Fiji Islands have a close phytogeographical affinity to New Caledonia.

SUBGENUS *TRACHYCOLEA* Spruce

Frullania ampullifera Jack ex Steph. Illustration: Hattori, 1981: 360, fig. 1.

MATERIAL EXAMINED—**Taveuni I.**: Southern tip of the island. On the NE slopes of the extinct Tavuyagea volcano, at 150–295 m alt. Corticolous in a *Barringtonia asiatica*-dominated mesic lowland forest on the outer crater slopes, at 250–295 m alt. *S. & T. Pócs 03293/F*. **Kadavu I.**: Central part, 2–3 km NNE of Vunisea, along the Namara Road, on the slopes at 120–165 m alt. Corticolous in secondary lowland rain forest on lilac volcanic soil. *S. & T. Pócs 03300/AJ*. On the coastal ridge, 0.5–1.5 km N of Vunisea, at 40–80 m alt. Corticolous in dry evergreen microphyllous forest with emergent *Gymnostoma vitiense* trees, many creeping *Flagellaria*, and with *Schizaea dichotoma* and Cyperaceae common in the ground layer. *S. & T. Pócs 03303/N, 03303/P*. In the first bay E of Vunisea on the southern coast, at 1–4 m alt. Corticolous in *Barringtonia asiatica* forest with transitions to dry evergreen microphyllous *Gymnostoma vitiense* forest. *S. & T. Pócs 03308/A, 03308/E*. On the isthmus of the island, at the sandy beach on the NW side of Vunisea Airport, 2 m alt. Shady, inner side of coconut (*Cocos nucifera*) trunk. *S. & T. Pócs 03011/A*. Western part of the island, 2 km NE of Tavuki village, at 150–175 m alt. Corticolous in dry evergreen microphyllous forest with emergent *Gymnostoma vitiense* trees on orange-red volcanic soil. *S. & T. Pócs 03309/B*.

DISTRIBUTION—This Fijian endemic was previously known only from its type locality on Ovalau I. and from two localities on Viti Levu I. (Hattori, 1985). It seems to prefer mesic or relatively dry habitats.

Frullania angulistipa Steph. Illustration: Hattori, 1981: 361, fig. 2.

MATERIAL EXAMINED—**Kadavu I.**: Central part, N of Vunisea, corticolous in dry evergreen microphyllous forest, 40–80 m. *S. & T. Pócs 03303/S*.

DISTRIBUTION—New to Fiji, hitherto was considered as an endemic of Samoa Islands, where was known only from type locality (Hattori, 1981). The Fijian specimen includes fertile

material containing perianths that certainly matches the Samoan species.

***Frullania* sp.** of unknown identity

MATERIAL EXAMINED—Taveuni I.: Bouma National Heritage Park, Tavoro Waterfalls, at 250 m alt. Epiphyllous in wet rain forest. *J. Eggers FID 2/29*. Morphologically it seems very close to the described but poorly known *Frullania cranialis* (Hook. & Taylor) Taylor in Gottsche et al. (illustration: Hattori, 1983: 138, fig. 52). *Frullania cranialis* stands very near to *Frullania dilatata* (L.) Dumort and otherwise only known from the type specimen at a locality in Australia where it has not been found since. The record of this taxon from New Zealand is erroneous (Hattori, 1983). According to the opinion of von Konrat (in litt.), further collections from the type locality as well as from the Fijian habitat are required in order to adequately determine the identity of this entity.

***Frullania ericoides* (Nees) Mont.** Illustrations: Vanden Berghen, 1976: 162, fig. 39. Schuster, 1992: 230, fig. 881.

MATERIAL EXAMINED—Viti Levu I.: Northeastern coast in the dry evergreen forest belt, SSE of Namarai village, at 50–60 m alt. On roots in riverine (gallery) forest. *S. & T. Pócs 03264/C*.

DISTRIBUTION—New to Fiji Islands. Widespread pantropical species.

***Frullania novocurvirostris* S. Hatt.** Illustration: Hattori, 1981: 370, fig. 8.

MATERIAL EXAMINED—Kadavu I.: Western part, 2 km NE of Tavuki village, at 170–200 m alt. Corticolous in dry evergreen microphyllous *Gymnostoma vitiense* forest. *S. & T. Pócs 03304/N*.

DISTRIBUTION—Known only from Fiji Islands (Ovalau I.) and from New Caledonia.

New Species

***Frullania vivipara* Pócs, sp. nov. (Subgenus *Diastoloba*).** Figures 1–21.

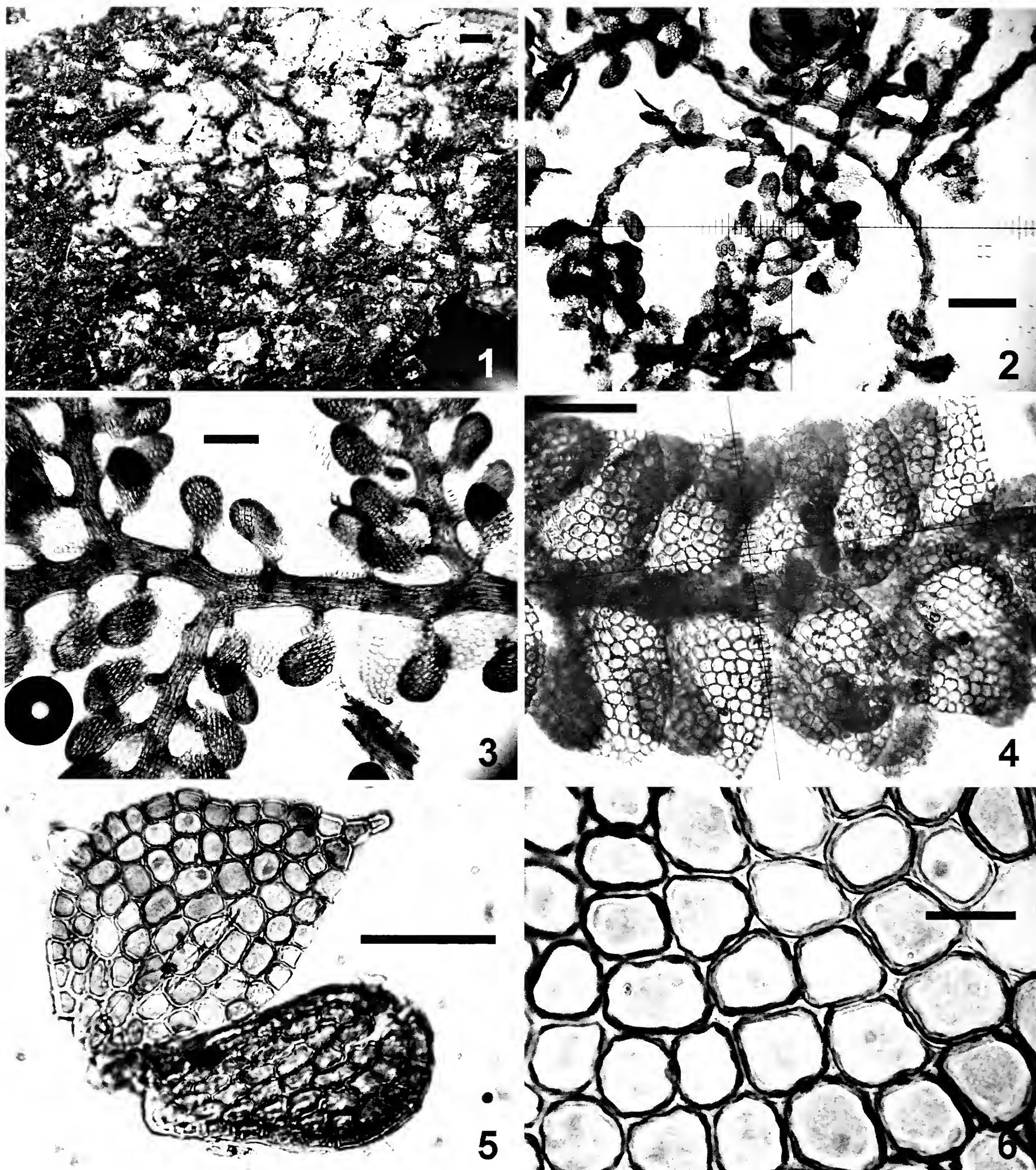
Planta rufo-brunnea, corticola, caulibus irregulariter ramosis, 50–80 μm crassis, saepe denudatis, ad 15 mm longis surculis 0.3–0.4 mm latis, foliis distantibus vel contiguis, caducis. Lobus folii oblonge-ovatus, 150–260 μm longus et 100–150 μm latus, apice acute vel obtusiusculo, cellulis medianis subquadrangularibus

diametro 18–25 μm trigonis parvis, Lobulus lobum fere aequilongus, clavatus, cum cellula lucida et cellulis uniseriatis hyalinis ad marginem ostii. Stylus uniseriatus, 4–5 cellularis, ad lobulum adhaerens. Amphigastria caulina parva, caulem fere aequilata, ad dimidium bilobata lobis basi 2–4 cellulae latis et 5–7 cellulae longis apicibus cellulis 1–3 uniseriatis. Dioica, adroecia lateralialia, 2–3 jugata, gynoecia terminalia in caule, foliis perichaetialis biseriatis bracteis et bracteolis marginibus irregulariter ciliato-dentatis. Perianthium dimidiate exsertum, obpyriformis, 600 μm longum et 300 μm latum tricarinatum carinis levibus et rostris 60–70 μm longis.

Similis *Frullaniae meijeri* Hattori (1974b) et *Frullaniae huerlimannii* Hattori (1976b), sed bene differt duabus foliis omnis caducis et lobulis ad marginem ostii hyalino-marginatis.

HOLOTYPE: Western part of **Kadavu** (Kandavu) **I.:** 2 km NE of Tavuki village, at 170–200 m alt., on *Gymnostoma vitiense* (Casuarinaceae) bark in dry evergreen microphyllous forest on orange-red volcanic soil. *Schizaea dichotoma* and Cyperaceae common in the ground layer. 19°03.829–04.102'S, 178°07.771–921'E. Coll. *S. & T. Pócs 03304/G*, 13 Sept. 2003 (EGR); isotype: F.

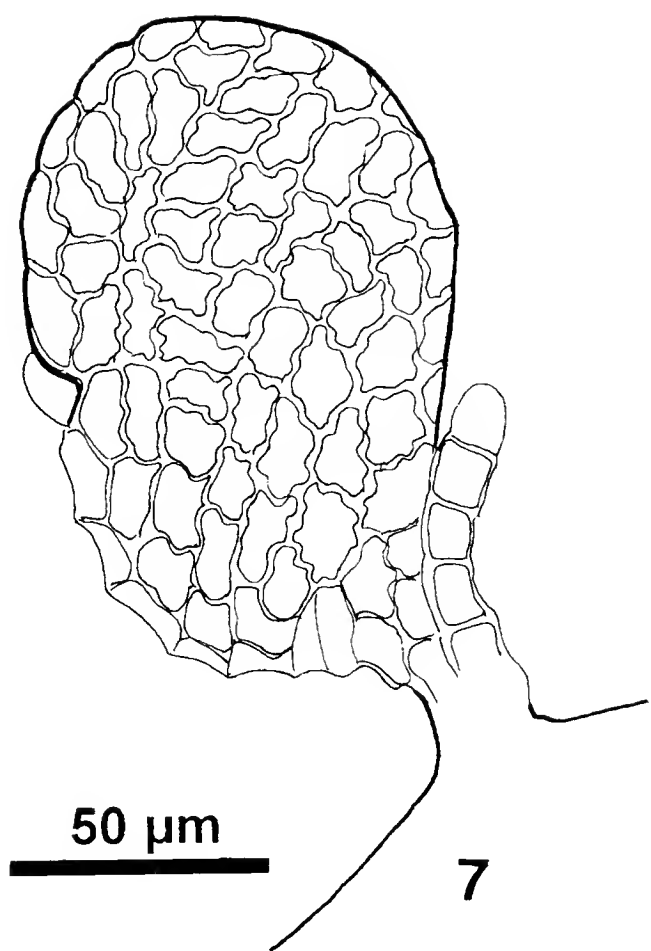
Minuscule, reddish-brown (in shady habitat sometimes green) plant creeping on bark, often forming dense mats of 1–2 cm diam. Shoots 5–15 mm long and 0.3–0.4 mm wide with irregular branching, stem 50–80 μm diam., in all older parts naked as all leaves caducous, only the underleaves persistent. Branches *Frullania*-type, initial branch appendages of *Ptychantha*-type according to the categories of von Konrat and Braggins (2001), i.e., the first branch underleaf consist of one ventral segment with an uniseriate appendage (sometimes also with a lateral tooth) and the first branch leaf has two saccate segments. Leaves distant or contiguous, 150–260 μm long and 100–150 μm wide, all caducous. Lobe ovate or elongato-ovate, with acute, slightly incurved, sometimes obtuse apex, median cells subquadrangular, 18–25 μm diam., walls slightly incrassate with small trigones and intermediate thickenings. Lobule more or less the same length as the lobe, clavate, with cellula lucida, spreading at an angle of 30–50° from the stem, asymmetric, the mouth margin slightly denticulate and consists of a row of hyaline cells. Stylus consisting of 4–5 uniseriate cells, tipped by a hyaline papilla, adherent to the proximal lobule base. Underleaves as wide as the stem, bilobed to half length, the lobes parallel, 2–4 cells wide at their base, 5–7 cells long, ending in an uniseriate apex consisting of 1–3 cells. Dioicous, androecia



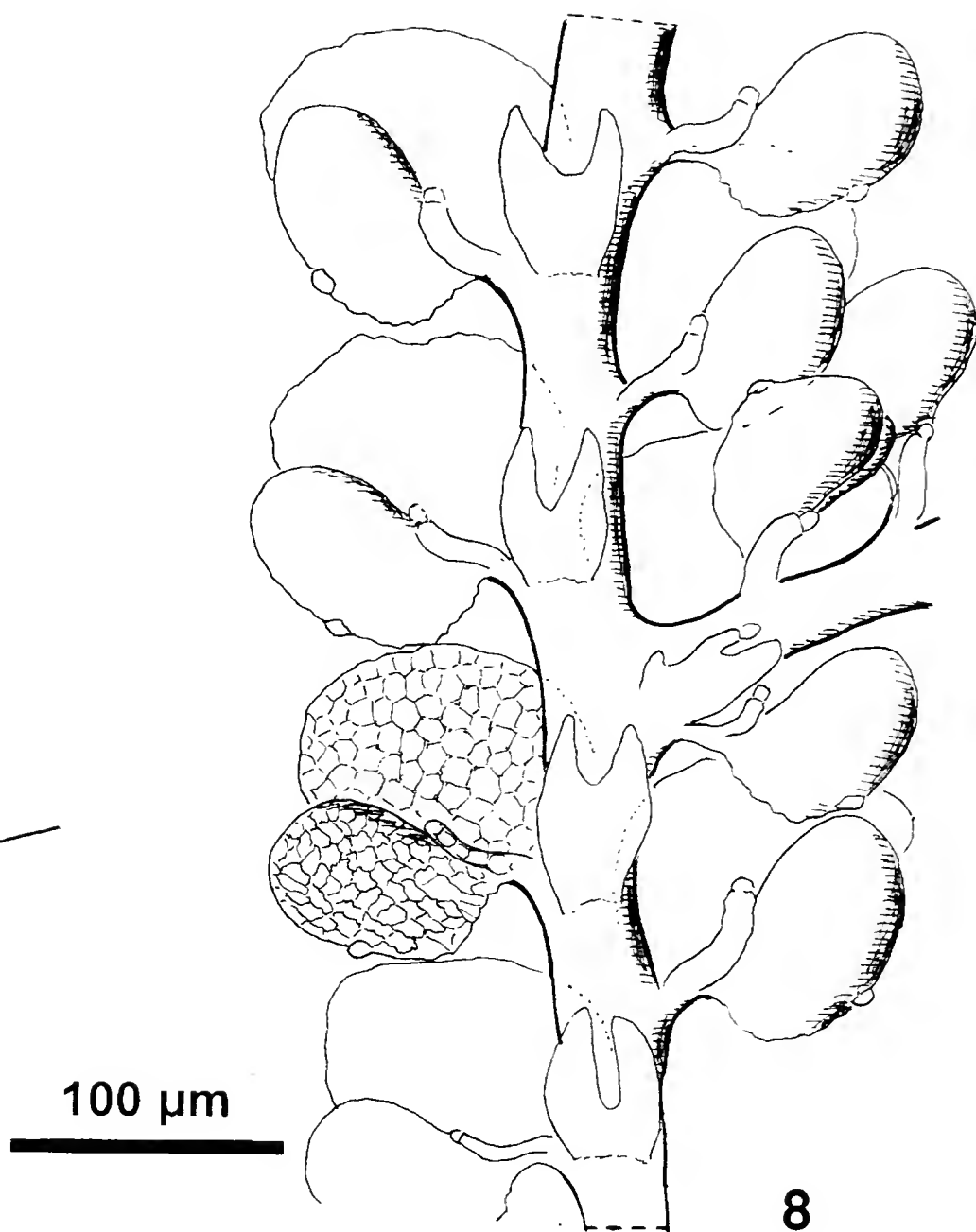
FIGS. 1–6. *Frullania vivipara* Pócs. All photos are made from the holotype. 1. Habit, dorsal view, among natural conditions, on bark. Scale bar = 1 mm. 2. Habit, ventral view. Scale bar = 250 μm . 3. Habit, ventral view. Scale bar = 100 μm . 4. Habit, dorsal view. Scale bar = 100 μm . 5. Leaf. Scale bar = 100 μm . 6. Median lobe cells. Scale bar = 20 μm .

on short lateral branches on the stem, much wider than long, consisting of 2–3 pairs of bracts. Gynoecia terminal on the stem, bracts and bracteoles in two whorls, their margin with long, irregular ciliate teeth. Perianthium obpyriform, partly exserted, 600 μm long and 300 μm broad, with a 60–70 μm long, parallel-sided, cylindrical

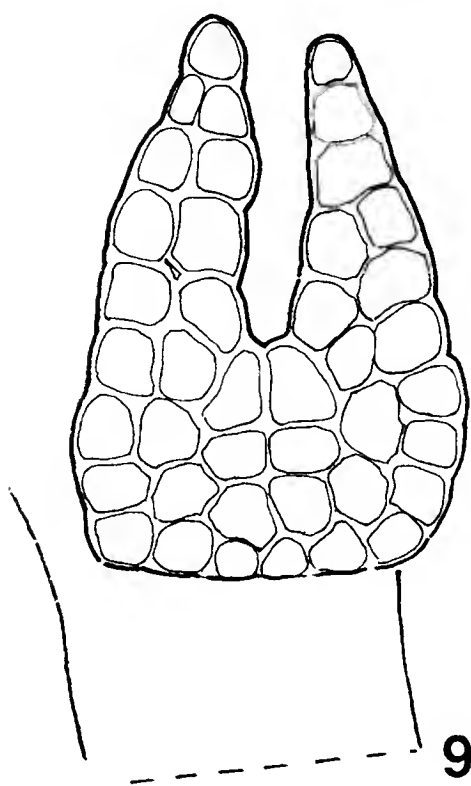
beak. Vegetative reproduction by the caducous leaves, which freely germinate from the bulging marginal cells. On one leaf sometimes more than one gemmaling can develop. Caducous leaves on propagative flagelliform shoots are not too rare among *Frullania*, e.g., on the North American *Frullania bolanderi* Aust., and caducous leaves on



7

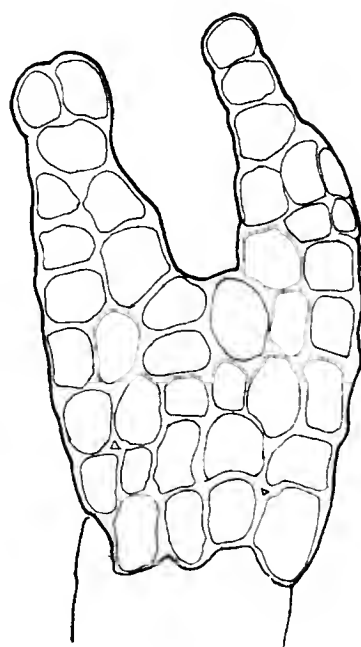


8

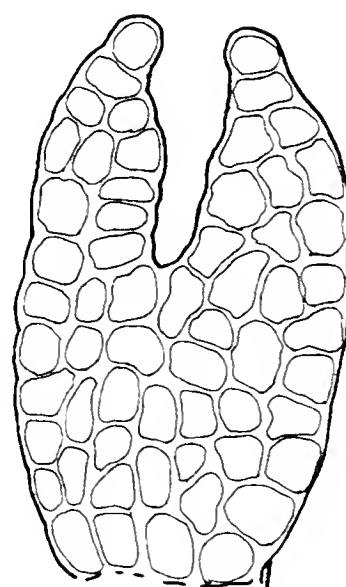


9

50 μm



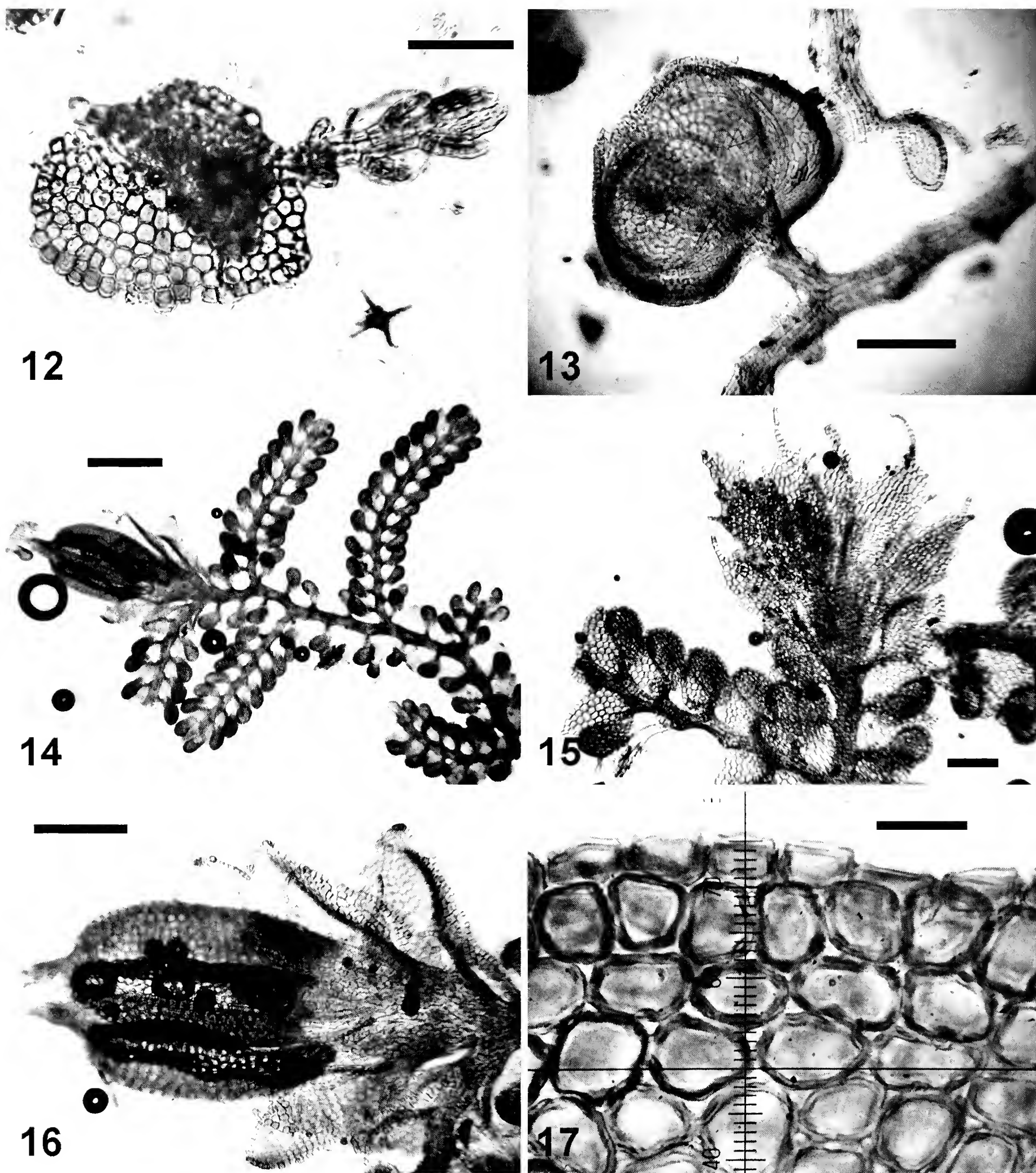
10



11

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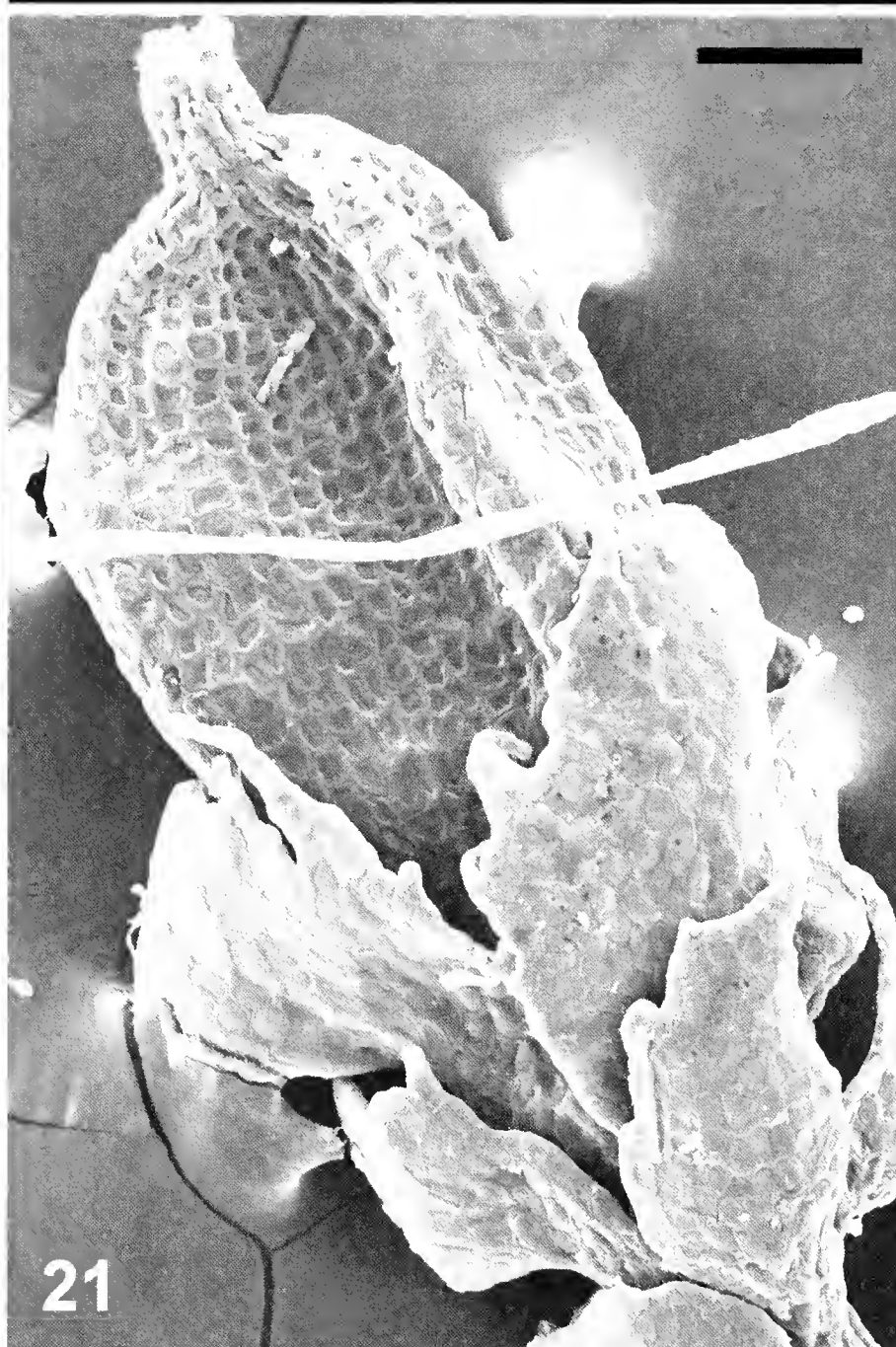
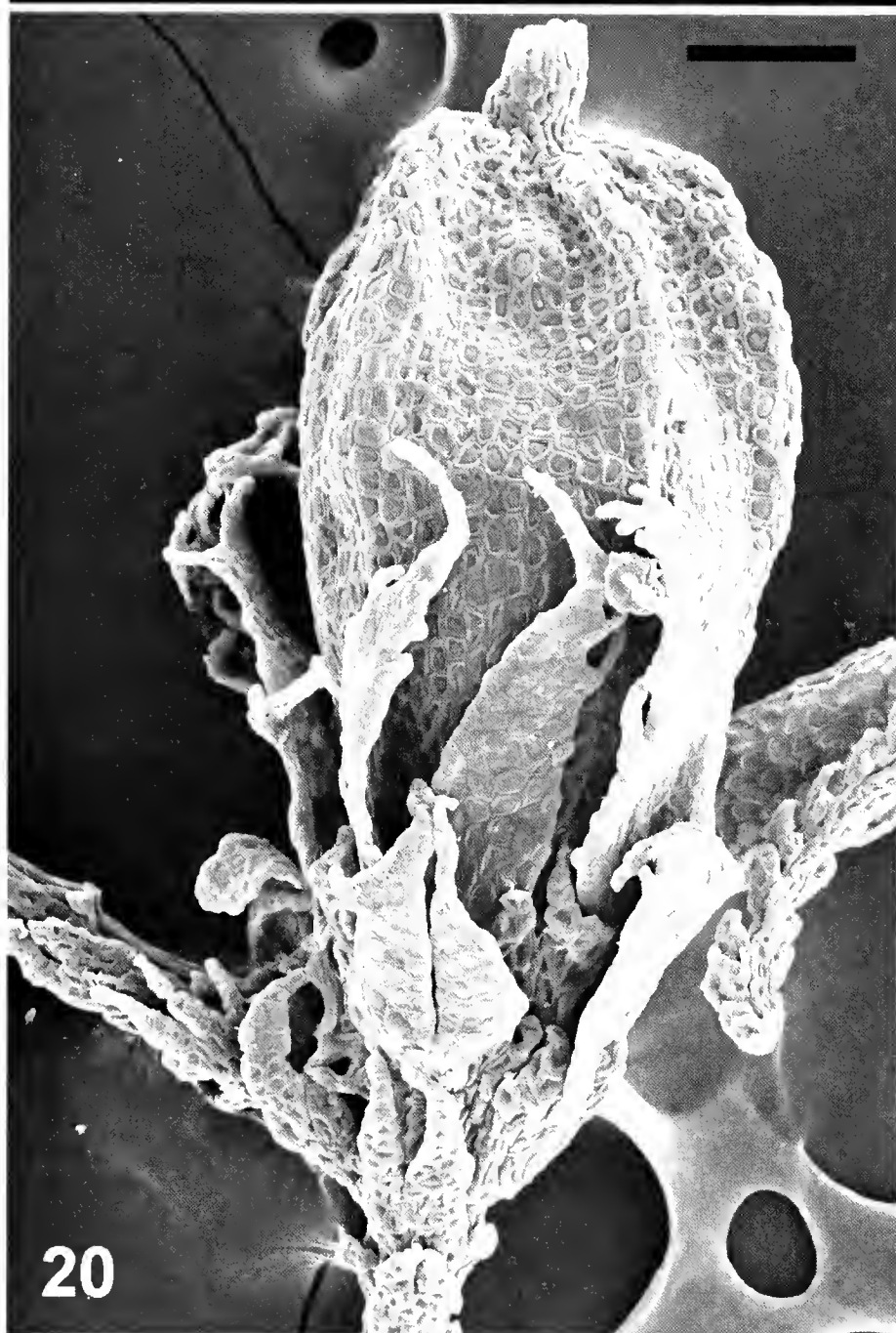
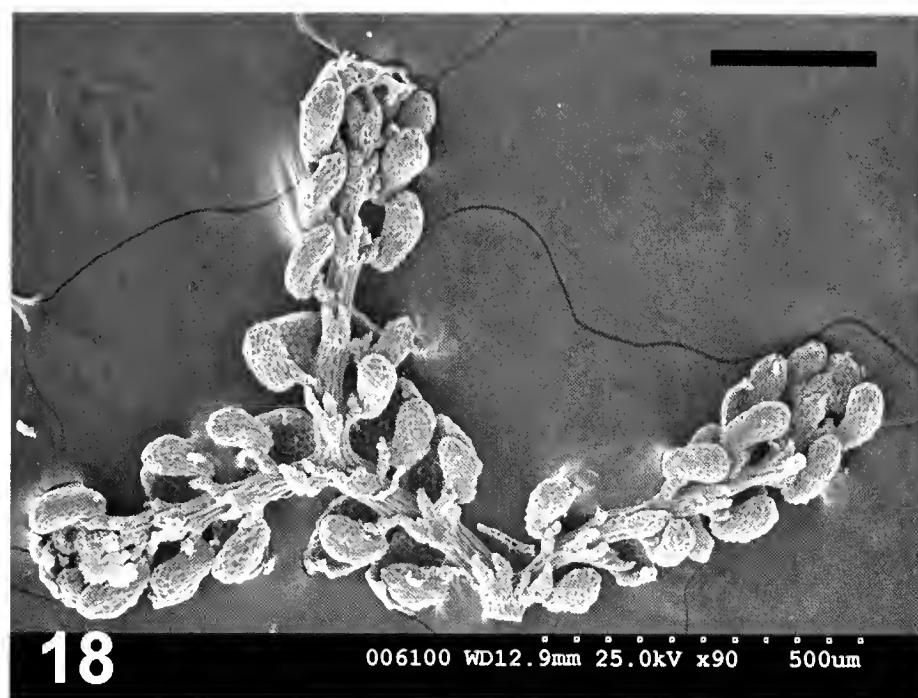
FIGS. 7–11. *Frullania vivipara* Pócs. Drawings made from the holotype. 7. Lobule. 8. Habit, ventral view. 9–11. Underleaves.



FIGS. 12–17. *Frullania vivipara* Pócs. **12.** Gemmaling, germinating from a marginal cell of caducous lobe. Scale bar = 100 µm. From the holotype. **13.** Male branch. Scale bar = 100 µm. From the holotype. **14.** Female plant. Ventral view. Scale bar = 250 µm. From S. & T. Pócs 03305/Y. **15.** Gynoecium. Scale bar = 100 µm. From S. & T. Pócs 03304/D. **16.** Perianth. Scale bar = 100 µm. From S. & T. Pócs 03304/D. **17.** Perianth cells along carina. Scale bar = 20 µm. From S. & T. Pócs 03304/D.

the normal stem or branches also occur to serve for vegetative propagation, e.g., on the African *Frullania obscurifolia* Mitt., but the case in which all leaves can be caducous with age, as in *F. vivipara*, is really rare. In all circumstances the underleaves used to remain on the stem.

OTHER SPECIMENS SEEN—Central part of **Kadavu** (Kandavu) **I.**: On the coastal ridge, 0.5–1.5 km N of Vunisea, at 40–80 m alt., in dry evergreen microphyllous forest on lilac volcanic soil. 19°02.390–529'S, 178°09.554–608'E. Coll. S. & T. Pócs 03303/AO. On the ridge SE of Vunisea telecom tower at 100–120 m alt., on



FIGS. 18–21. *Frullania vivipara* Pócs. **18.** Habit, ventral view. From the holotype. **19.** Nedudated stem and branch with underleaves. From the holotype. **20.** Perianth, ventral view. Scale bar = 100 μ m. From the holotype. **21.** Perianth, dorsal view. Scale bar = 100 μ m. From the holotype.

lilac volcanic soil. 19°03.214–300'S, 178°09.836–877'E. On bark of emergent *Gymnostoma vitiense* (Casuarinaceae) trees, in dry evergreen forest similar to the previous ones. S. & T. Pócs 03303/AO. 12 Sept. 2003 (EGR). Western part of **Kadavu I.**: 3 km NNE of Tavuki village, on a ridge at 220–240 m alt. Corticolous in dry evergreen microphyllous forest with transitions to

mesic evergreen rain forest on orange-red volcanic soil. 19°03.621–678'S, 178°07.743–844'E. S. & T. Pócs 03305/Y, 13 Sept. 2003 (EGR, SUVA); same locality as the type, on decaying wood S. & T. Pócs 03304/D (EGR).

HABITAT AND ECOLOGY—As already mentioned in my previous paper in this issue (Pócs, 2008), the semidry evergreen microphyllous forests of

Kadavu Island, dominated by *Gymnostoma vitiense* (Casuarinaceae), provide a very special habitat for many interesting hepatic species. The forest is relatively dry with a quite open canopy in spite of the high precipitation and air humidity, due to the seasonality of rainfall distribution. According to Mueller-Dombois and Fosberg (1998), this type of semidry forest was much more distributed in the less rainy parts of larger islands but became the first victim of the spreading agriculture. On Kadavu Island, the probably ultrabasic, bright lilac or orange-red soils contributed to the climatic effects and, luckily enough, the relatively sparse human population spared most of this type of forests. Species of *Frullania* favor this kind of habitat, as we could see from the above enumeration. Some rare species (*F. angulistipa*, *F. novocurvirostris*) and even the above new species occur exclusively here.

AFFINITIES AND DIFFERENTIATION—The new species shows obvious affinity to two other members of subgenus *Diastoloba*, namely to *Frullania meijeri* Hattori (1974b, figs. 1–2) from Borneo and to *Frullania huerlimannii* Hattori (1976b, fig. 2) from New Caledonia, by their small size, pointed, falcate lobes subequal to the lobules in length, by their narrow underleaf, and by their fimbriate bracts. However, *F. meijeri* is distinct by its mamilliose lobe cells and *F. huerlimannii* by its funnel-shaped perianth beak. On the other hand, *F. vivipara* differs from both of them (and from most members of subgenus *Diastoloba*) by the fact that all leaves are very caducous, and each can grow gemmalings at its margin. The older parts of weft consist mostly of naked stems with the only persistent underleaves. Another distinctive feature of the new species is the lobule, margined by a row of hyaline cells.

Phytogeographic Evaluation

The 26 *Frullania* species known from Fiji Islands gives an idea about the phytogeographic affinity of the genus in these islands. The following list attempts to classify the species into different area groups:

1. <i>F. ampullifera</i>	Endemic
2. <i>F. angulistipa</i>	Fiji, Samoa
3. <i>F. apiculata</i>	Palaeotropical
4. <i>F. auriculata</i>	Endemic
5. <i>F. baladina</i>	New Caledonia, Fiji
6. <i>F. capillaris</i>	New Caledonia, Fiji

7. <i>F. chevalieri</i>	New Caledonia, New Zealand, Fiji
8. <i>F. deflexa</i>	East Melanesian (New Caledonia, Vanuatu, Fiji, Samoa)
9. <i>F. epiphylla</i> ssp. <i>fijiensis</i>	Endemic subspecies
10. <i>F. ericoides</i>	Pantropical
11. <i>F. gaudichaudii</i>	Indomalayan–Pacific + South American
12. <i>F. gracilis</i>	Indomalayan–Pacific
13. <i>F. hamata</i>	Melanesian (New Guinea, Bismarck I., Fiji)
14. <i>F. hypoleuca</i>	Indomalayan–Pacific
15. <i>F. immersa</i>	Melanesian (New Guinea, Vanuatu, Fiji, Samoa)
16. <i>F. intermedia</i>	Indomalayan–Pacific
17. <i>F. neurota</i>	Southeast Asia, Indomalaya, Hawaii, Mexico
18. <i>F. nodulosa</i>	Pantropical (lowland rain forest)
19. <i>F. novocurvirostris</i>	New Caledonia, Fiji
20. <i>F. parhamii</i>	Endemic
21. <i>F. serrata</i>	Palaeotropical
22. <i>F. ternatensis</i>	Indomalayan–Pacific
23. <i>F. trichodes</i>	Indomalayan–Pacific
24. <i>F. vaga</i>	Endemic?
25. <i>F. vivipara</i>	Endemic

In the *Frullania* flora of the Fiji Islands, the number of endemics is quite high; this is the most numerous group, with six species. The next highest group is formed by the Indomalayan–Pacific element, with five species. The number of species occurring jointly in New Caledonia and in the Fiji Islands is four, and the number of species with a Melanesian distribution is three. There is one species known only from Fiji and Samoa, there are two species with an Asian–Oceanian–American disjunct distribution, two species with a Palaeotropical (Afro–Asian–Oceanian) distribution, and two species with a pantropical distribution.

The high proportion of *Frullania* endemics in Fiji (24%) is comparable with the proportion of endemic *Frullania* in New Caledonia (29 of 48 = 60%, based on Iwatsuki [1990], modified). The high proportion of *Frullania* endemics in Fiji of 24% compares to that of 60% (29 of 48, based on Iwatsuki [1990], modified) for New Caledonia. According to Hattori (1982), 48 of the 77 species (62%) of *Frullania* are endemic to New Guinea.

The endemism can be very different, depending on the age of the area and the taxa, the evolutionary history, and the dispersal ability of the concerned taxonomic groups (Piippo & Koponen, 1997). The endemism of mosses in New Guinea, for example, is only 18% according to Hyvönen (1989). Naturally, after further revisions and monographic study takes place in those regions, the number of endemics may be reduced.

Another remarkable group is formed by those species occurring only in New Caledonia and on the Fiji Islands (4 of 26 = 15%), exceeding the number of Melanesian species. This may be the result of an old plate tectonic link between the two areas or long-range air dispersal; the distance between the two centers is 1250 km and the Vanuatu Islands could serve as stepping stones. However, the general east–west direction of the jet-currents does not favor air dispersal from the very old land mass of New Caledonia toward the young volcanic surface of the Fiji Islands, which should have been the recipient in this case of these elements. A former land connection is another possibility, as there are small Gondwanan fragments in the region, e.g., 'Eua Island of the Tonga Archipelago, which were closer to Fiji and New Caledonia than they are currently (Mueller-Dombois & Fosberg, 1998). Floristically and biogeographically, the Fijian Islands are of great significance in the Pacific region, as they are composed of Australasian, Melanesian, and Polynesian elements that together contribute to its rich flora.

Certainly, based on the preliminary studies of the bryoflora, the Fiji Islands boast one of the highest rates of species richness and endemism in the region, and can be considered a bryological hot spot, along with New Caledonia, that was designated by Tan and Pócs (2000). At the same time, it is clearly seen from the number of new records how still poorly known is the bryoflora of these (and probably also of the other) South Pacific islands.

Acknowledgments

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Natural History Museum with a Hitachi S-2600 N type SEM, with the help of Dr. Krisztina Buczkó. Thanks are due to Matt von Konrat (F) for identifying our *F. chevalieri* collection and for his valuable advice in the whole treatment, also to Jens Eggers placing at our disposal his specimens, furthermore. Last but not least, I am very grateful to the late Dr. Sinske Hattori, who kindly supplied me with all his valuable publications on Southeast Asian, Australasian, and Oceanian *Frullania*.

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FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Six: Liverwort Floristics and Revisions—Asia and Australasia

Chapter Fourteen: *Mnioloma* (Calypogeiaceae: Jungermannopsida) in Australasia: how many species are there?

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Abstract

We recognize three species of *Mnioloma* for Australasia. *Mnioloma novaezelandiae* J.J.Engel is known only from New Zealand. The plants upon which the Australian record of *M. novaezelandiae* was based are referred to *Mnioloma* cf. *fuscum* (Lehm.) R. M. Schust., for, while similar to this species, we have been unable to substantiate their placement either within this species or as a separate entity. We describe *Mnioloma stamatotonum* as new for plants with crenulate leaf margins, ovate leaves, and underleaves with irregular margins. This plant is known from two specimens, one from Mt. Lewis (Queensland, Australia), the other from Mt. Kouakoué (New Caledonia). *Mnioloma novaezelandiae* appears to display considerable clinal variation, the quantification of which would inform the grouping decisions we make here.

Introduction

The genus *Mnioloma* was initially described as a monotypic entity, based on *M. rhynchophyllum* Herzog, a species from Costa Rica (Herzog, 1930). It was subsequently reduced to a subgenus of *Calypogeia* by Bischler (1963) and then reinstated by Schuster (1995) whose circumscription encompassed two of Bischler's three subgenera whilst retaining their status (subg. *Caracoma* (Bischl.) R.M.Schust. and subg. *Mnioloma* Herzog). This small genus of ca. 13 taxa has been considered Neotropical and occurs mostly in northern South America, Central America, and the West Indies, with the exception of *M. fuscum* which is "imperfectly circumtropical" (Schuster, 2000), being recorded from a number of other places (Grolle, 1977; Kitagawa, 1988; Pócs, 2005), and *M. caespitosum* (Spruce) R. M. Schust. which is reported from Mt. Kilimanjaro as well as South America (Pócs, 2005). Recent work has extended the range of the genus into New Zealand (Renner, 2003), where one other species, *M. novaezealandiae* J. J. Engel, is currently known (Engel, 2006). Renner and Braggins (2006) reported *M. novaezealandiae* from northern Queensland, Australia, on the basis of material collected recently from Mt. Bartle Frere in the Wet Tropics.

Here we report a second species of *Mnioloma* for Australia, from Mt. Lewis (with this species also being reported as new for Mt. Kouakoué, New Caledonia). We also reexamine the Bartle Frere material upon which the earlier Australian record of *M. novaezealandiae* was based and find this report in error. The two species of *Mnioloma* in Australia are each known from a small number of specimens from Queensland, one from Mt. Lewis and two from Bartle Frere. *Mnioloma novaezealandiae* is currently known from four specimens, including the type from Fiordland (Engel, 2006). The small quantity of available material makes an adequate appraisal of patterns of variation, and hence similarities and differences between specimens, difficult. As all material is sterile, we are further limited to gross morphological characters of the gametophyte.

One of the underlying tenets of science is that the collection, analysis, and interpretation of data should be repeatable and independently verifiable by other workers. Writing about characters and character states in biology, Stevens (2000) remarked that observed differences between taxa are often the result of "poorly understood

and very individualistic cognitive-psychological decisions involving decisions based on particular groups of observations." For example, discontinuities identified as substantiating the segregation of two or more specimens into two different species may be a by-product of small sample size, and not reflective of species boundaries. Maximizing the testability of hypotheses of interindividual relationships can be achieved primarily through an evidence-based approach, wherein data supporting the differences are presented as a component of the evidential basis for species recognition.

Liverworts are generally character-poor, and differences between similar taxa rest primarily on perceived discontinuities in quantitative structures. Taxa also frequently exhibit considerable phenotypic variation, with the result that descriptions employing imprecise measurements are difficult to interpret satisfactorily, e.g., "*Lejeunea patens* is a paler plant than *L. cavifolia*; the lobes of its leaves spread more abruptly from the lobules and are more convex, especially when dry; the underleaves are more nearly orbicular and are smaller than the lobules" (Evans, 1902: 153). In addition, considerable use of shape has been made as a source of differences between groups of species. However, no studies have yet quantified these shape-based differences in an objective and repeatable fashion that allows the use of statistical methods.

Morphological variation in single specimens is not necessarily representative of morphological variation of the species to which they belong. Having only a single specimen available for study precludes assessment of interpopulation variation (and possibly even interindividual variation if the material is clonal). To counter the incomplete knowledge of patterns of variation at the species level, it is necessary to have as complete as possible knowledge of specimen-based patterns of variation. This should maximize the chance of detecting not only bridging morphological variation between specimens but also any differences obscured by the lack of discontinuities. Multivariate analysis is an excellent tool for identifying and localizing differences between groups of data points.

In this paper, we aim to provide the baseline data against which future collections can be compared, with the ultimate aim of being able to accept or reject the hypothesis that there are two entities present in Australia and that they differ

from New Zealand material. As the size and shape of lateral and ventral leaves are of considerable importance in distinguishing species of *Mnioloma*, we present an allometric and morphometric study of these characters in four *Mnioloma* specimens from Australia, New Zealand, and New Caledonia, including an isotype of *M. novaezealandiae*. We performed a multivariate analysis of allometric variation, and an elliptical Fourier analysis of variation in leaf and underleaf shape on the limited suite of material available to us in an attempt to identify patterns of variation and search for strict morphological discontinuity.

This paper acknowledges the contribution John Engel has made to knowledge of the Australasian hepatic flora, and in this instance to *Mnioloma*.

Materials and Methods

Four specimens were included in our multivariate analysis of size and shape. These four specimens were selected on the basis of availability and their ability to withstand invasive examination. They were grouped into three *a priori* groups on the basis of gross morphology and their possession of qualitative characters described below.

We selected between 10 and 15 shoots from each specimen and slide mounted these in glycerol–glycerine following the protocol presented by Zander (1997). Images of 30 lateral leaves and 30 underleaves for each specimen were captured using a digital camera and microscope (Leica IM300 with IM1000 software, Photomakroscop M 400). Measurements and outlines were derived from this suite of images. Leaf width and underleaf width were measured to provide a coarse quantification of size differences between specimens. We anchored the lateral leaf width dimension at the antical end of the stem insertion and measured this dimension perpendicular to the longest axis of the leaf. For underleaf width, the widest axis of each underleaf was measured. All dimensions were measured from digital images imported into ImageJ (Abramoff et al., 2004).

Our approach to sampling had two aims: (1) to quantify as completely as possible the breadth of variation exhibited by each specimen in order to maximize the probability of observing overlap or linkage in the form of intermediates in patterns of variation, and (2) to quantify shape-based differences in a form independently verifiable by other workers. This serves two purposes: it

removes any observer bias from the identification of discontinuities between specimens, and it allows testing of the hypotheses of similarity and difference we present (as identified discontinuities in support of the recognition of our taxa) against additional data from further specimens as they are found. The small amount of material available in each specimen precluded the possibility of more sophisticated analyses investigating variation at similar developmental points on individual stems within and between specimens or within stem variation (which would have involved destructive techniques to obtain leaf measurements).

The methods we present here are accessible to all workers with access to a microscope, a digital camera, the World Wide Web, and a basic statistical package. While it can be easily argued that a square is unmistakably different from a circle, there are many intermediate forms that cause confusion, no matter how extensive the definitions supplied. The methods used here yield data upon which shape-based differences between groups of specimens can be identified and substantiated in an objective and repeatable fashion.

One-way analyses of variance (ANOVAs) were performed on both variables to test whether significant differences exist between specimens. On returning a significant result, we used both Scheffé's and Tukey's *a posteriori* tests (Brown, 2005) to localize any difference detected by ANOVA and identify groups comprising homogeneous subsets of specimens.

We measured and quantified shape differences in lobules and underleaves of the two specimens using SHAPE (Iwata & Ukai, 2002), which performs elliptical Fourier analysis of outlines, and principal components analysis (PCA) of elliptical Fourier descriptors normalized on the basis of the longest radius. This normalization was performed manually by orientating the long axis of the first ellipse along the line of the stem insertion for underleaves, and perpendicular to the stem insertion for leaves, to standardized the placement of the long axis. The Princomp executable in SHAPE was used (Iwata & Ukai, 2002) to perform a PCA on the normalized elliptic Fourier descriptors. Principal components analysis extracts and summarizes components explaining variation in distribution of samples in multidimensional space.

A discriminant function analysis was performed on a single data set that combined

the shape and size variables from leaves and underleaves. Discriminant function analysis reveals which attributes within a data set contribute most to differences between the specimens (James & McCulloch, 1990). Discriminant function analysis differentially weights characters in order to achieve maximal separation between predetermined groups. This weighting scheme is encapsulated in a discriminant function vector that can then be used to predict group membership of additional unknown specimens on the basis of the same kind of data. Leave-one-out cross-validation served as a partial test of the grouping capabilities of the discriminant function for each data set.

Results

Size

Significant differences exist between the four specimens for lateral leaf width ($F = 75.85$, $p < 0.0001$) and underleaf width ($F = 73.49$, $p < 0.0001$). However, the ranges of both overlap, so fail to yield strictly discontinuous groups of data points. *Post hoc* tests consistently separated *M. novaezealandiae* from the other three specimens, but otherwise failed to resolve our *a priori* groups.

Shape

Principal components analysis of leaf and underleaf shape scores (Figs. 1–4) fail to resolve discrete groups of data points, which means specimens display considerable overlap in shape of underleaves and leaves. The first two principal components for leaf shape, which together explain 78.96% of variation, are associated with a change in shape from oblong to ovate. The distribution of data points along these two axes suggest that specimens from New Caledonia and Mt. Lewis have rounder leaves than specimens from Fiordland (*M. novaezealandiae*) and Bartle Frere (Fig. 1). The first principal component for underleaf shape (Fig. 3), which explains 42.33% of variation, describes a trend where underleaves become increasingly squat in shape. Distribution of data points along this axis suggest that the Fiordland plant has generally squatter underleaves than the other three specimens, and that all specimens overlap considerably in

underleaf shape. These trends in shape differences can be observed in the lateral leaf and underleaf outline diagrams presented for each plant in Figures 5–8.

Discriminant functions analysis fails to resolve discrete groups, although separation of specimens is more complete than in any of the PCA plots (Fig. 9). The discriminant functions vector succeeds in classifying data points into groups corresponding with our *a priori* groups 88.0% of the time for *M. novaezealandiae*, 76.0% of the time for the Bartle Frere plant, and 86% of the time for the Mt. Lewis and New Caledonian plants. Leave-one-out cross-validation results are similar. The Bartle Frere plant is most frequently confused with *M. novaezealandiae*, and the Mt. Lewis plant with the Bartle Frere plant in both analyses.

Other Characters

A range of characters in the Australasian collections exhibit considerable uniformity, e.g., cell size, cell wall thickness, and trigone formation, and do not provide any separation/discontinuities between specimens. Other characters exhibit considerable variability, e.g., stem cross section (Figs. 10.8–10.9, 11.11–11.12); almost the full range of variation observed can be found within parts of the same stem). Although this measure may still be of use in future analyses, it presents considerable operational difficulties, e.g., angle of cut has a significant effect on measurements (but not cell counts), as does the amount of cell distortion occurring, and both are hard to control unless sectioning is done with a microtome. The remaining characters, such as the crenulation of the lateral leaf and underleaf margins, are hard to quantify, but material from Mt. Lewis and Mt. Kouakoué is more strongly crenulate and the cuticle is more heavily verruculose than in the Bartle Frere and Fiordland collections (but the measures for these characters fall within the error limitations of the graticules used, with the differences being statistically meaningless).

Discussion

For the most part, taxa within the genus *Mnioloma* have been defined using characters involving aspects of lateral and ventral leaf shape

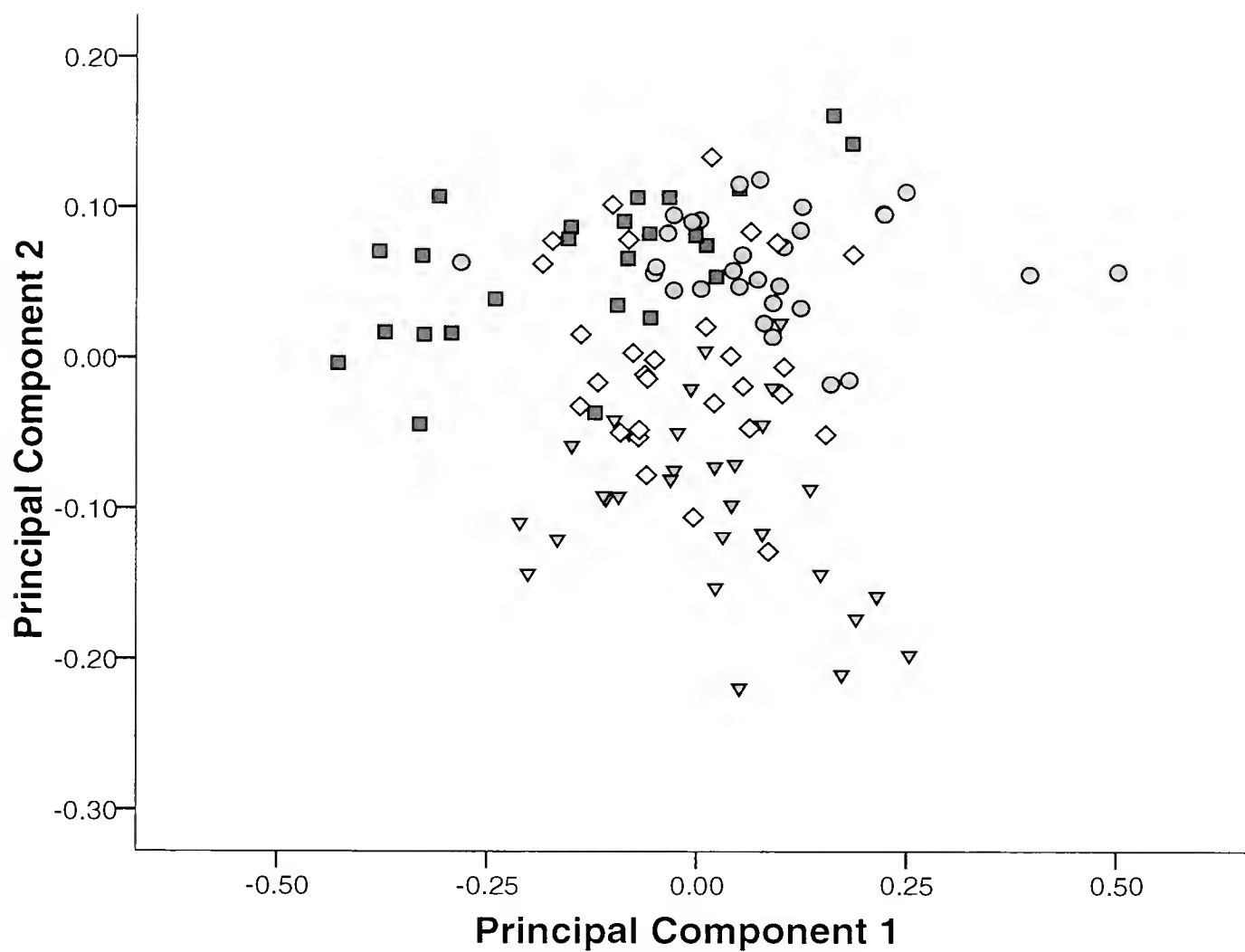


FIG. 1. First two principal components explaining variation in lateral leaf outline for four specimens of *Mnioloma*. ● = Bartle Frere. ■ = Fiordland. ▼ = Mt. Lewis. ◇ = Mt. Kouakoué.

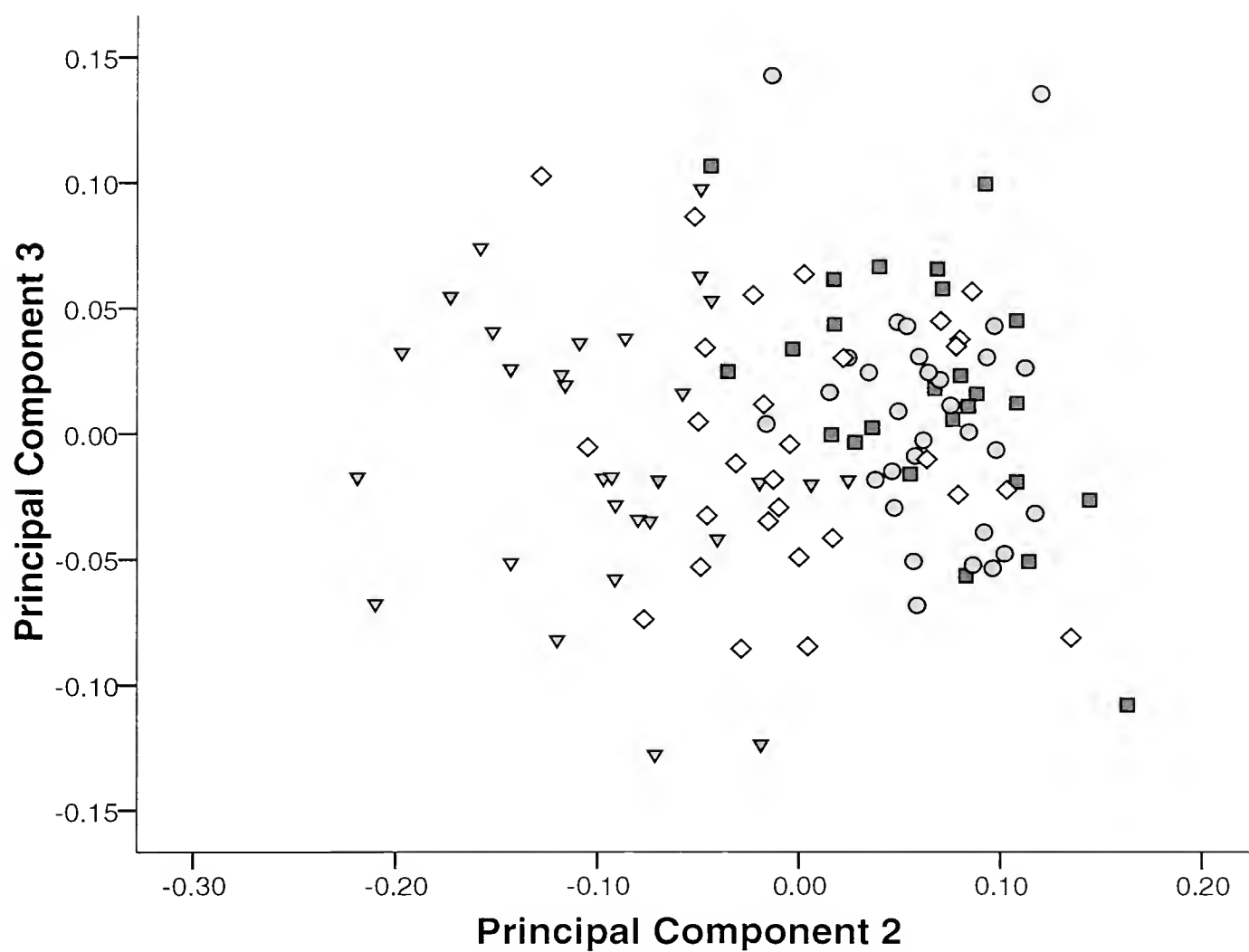


FIG. 2. Second and third principal components explaining variation in lateral leaf outline for four specimens of *Mnioloma*. ● = Bartle Frere. ■ = Fiordland. ▼ = Mt. Lewis. ◇ = Mt. Kouakoué.

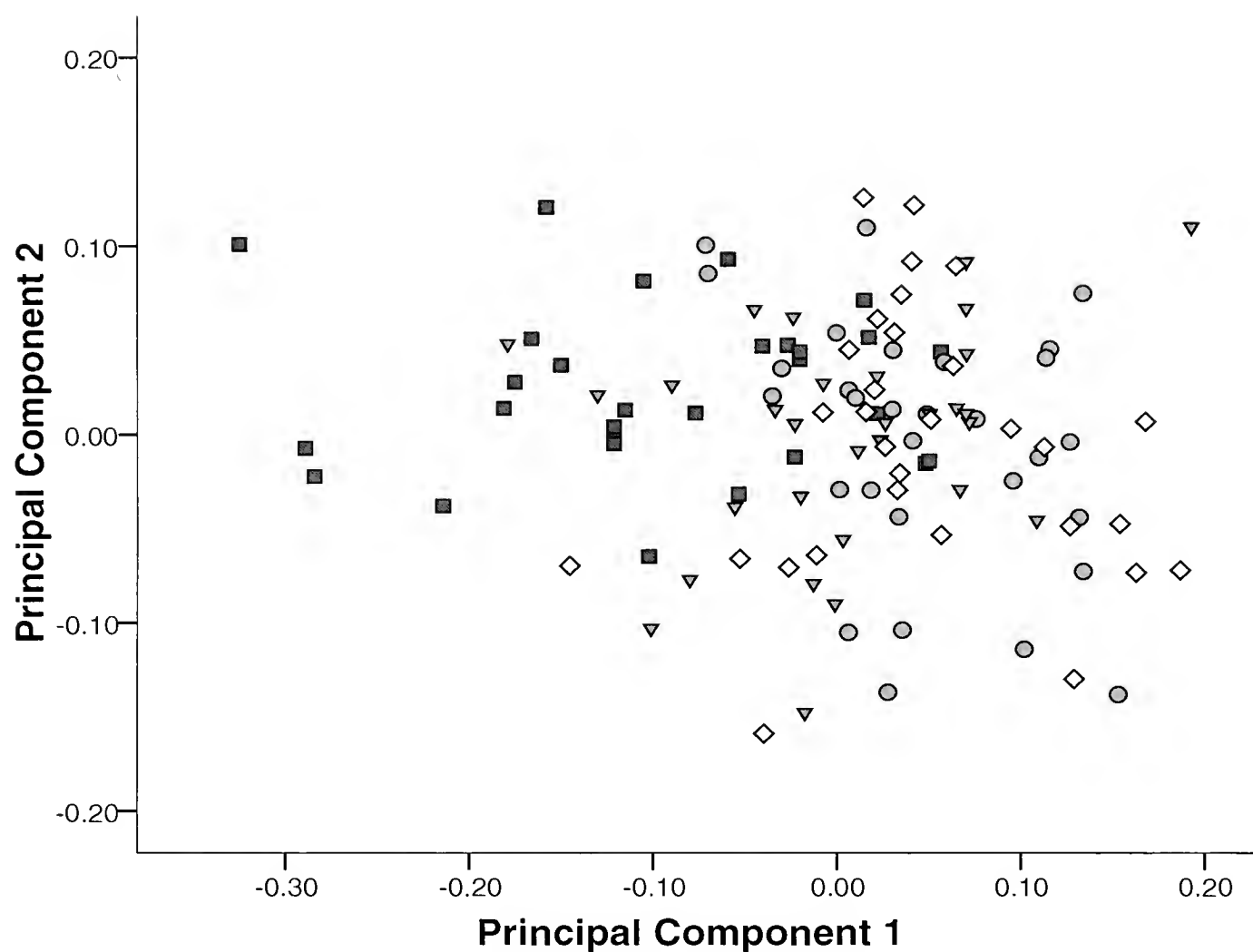


FIG. 3. First principal component explaining variation in underleaf outline for four specimens of *Mnioloma*. ● = Bartle Frere. ■ = Fiordland. ▼ = Mt. Lewis. ◇ = Mt. Kouakoué.

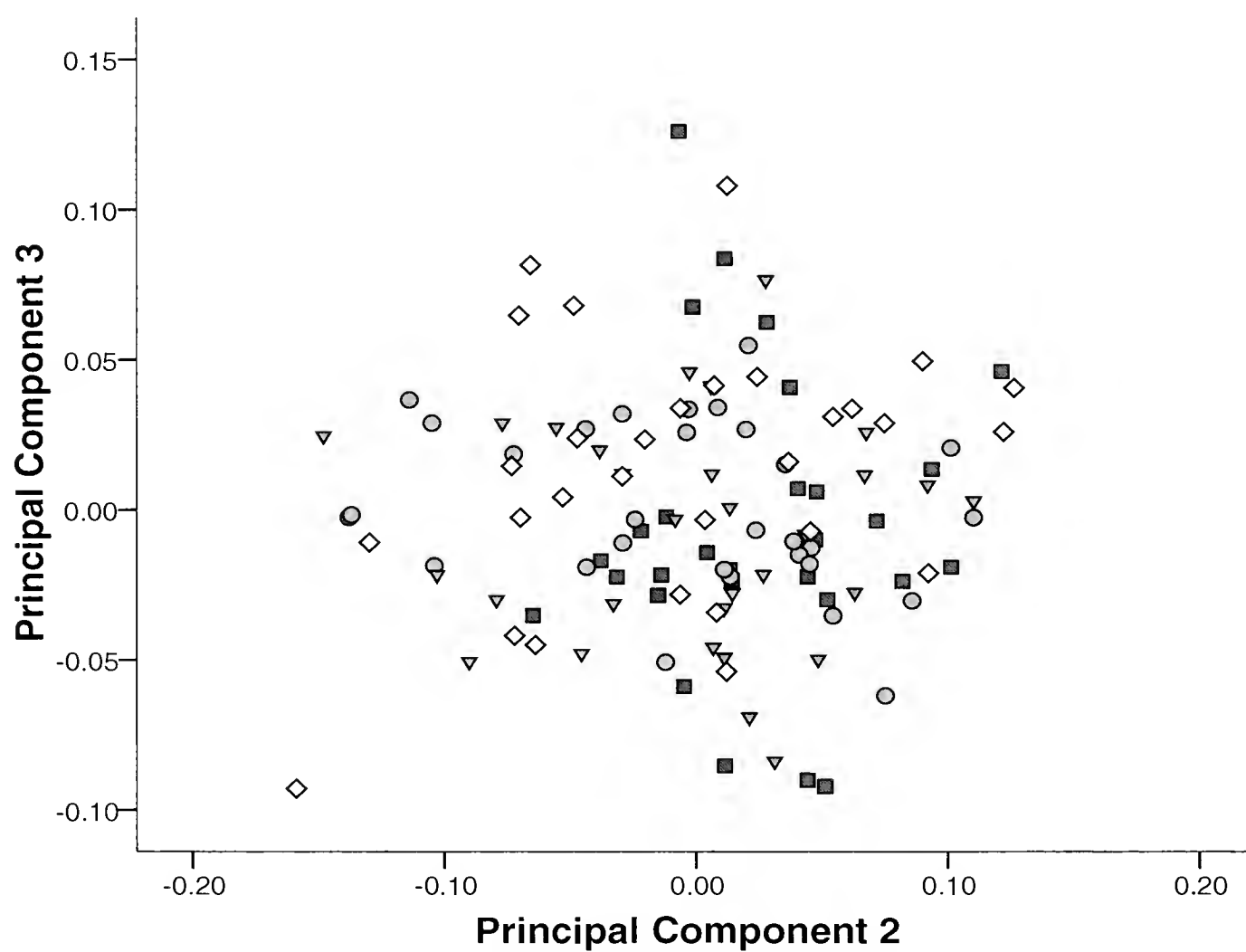


FIG. 4. Second and third principal components explaining variation in underleaf outline for four specimens of *Mnioloma*. ● = Bartle Frere. ■ = Fiordland. ▼ = Mt. Lewis. ◇ = Mt. Kouakoué.

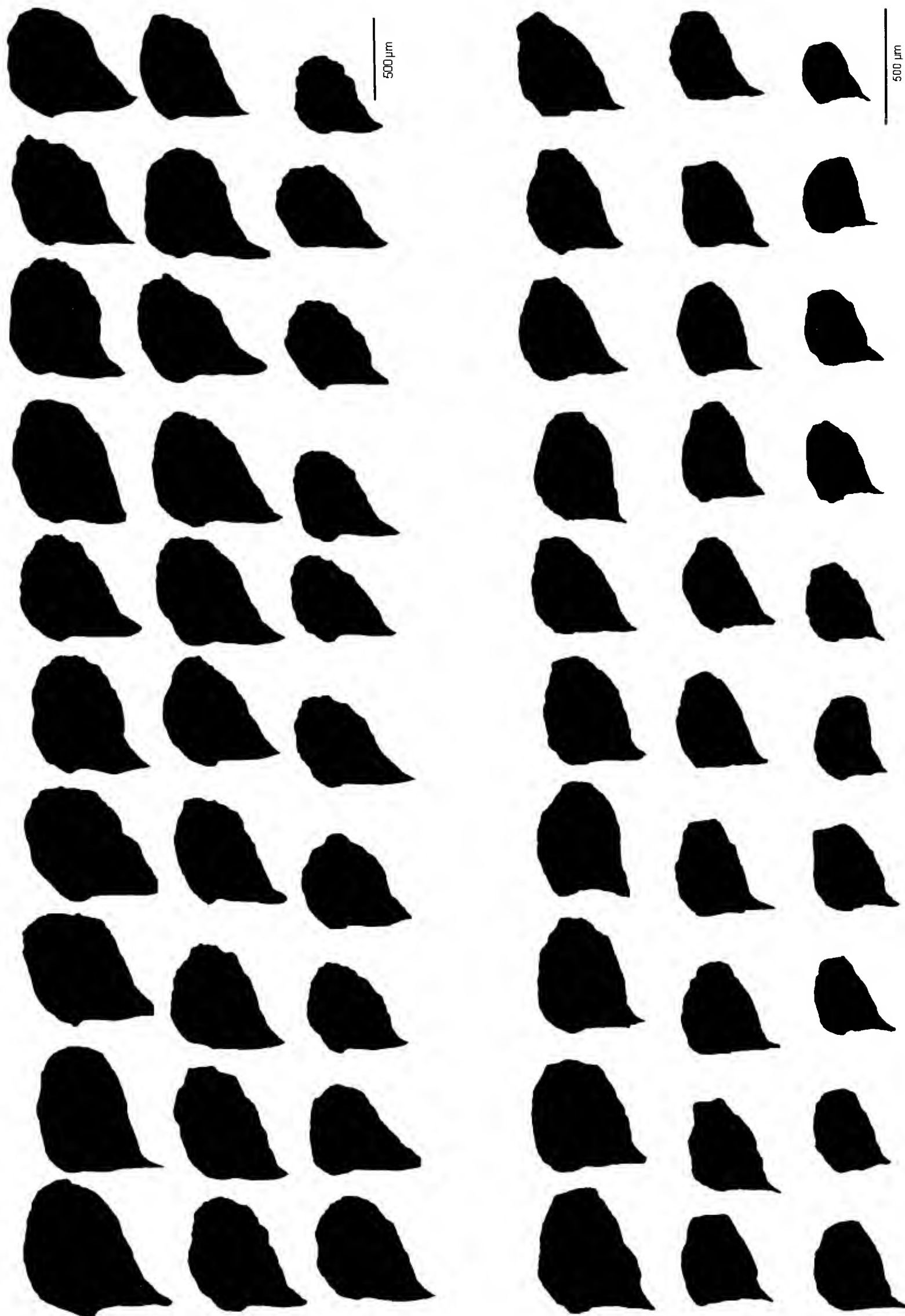


FIG. 5. Silhouettes of lateral leaves from the type collection of *Mnioloma novaezelandiae* (upper 30 leaves; Renner CMS 1156 T/10, CHR) from Fiordland, New Zealand, and *M. cf. fuscum* (lower 30 leaves) from Bartle Frere, Queensland, Australia (Renner 2219).

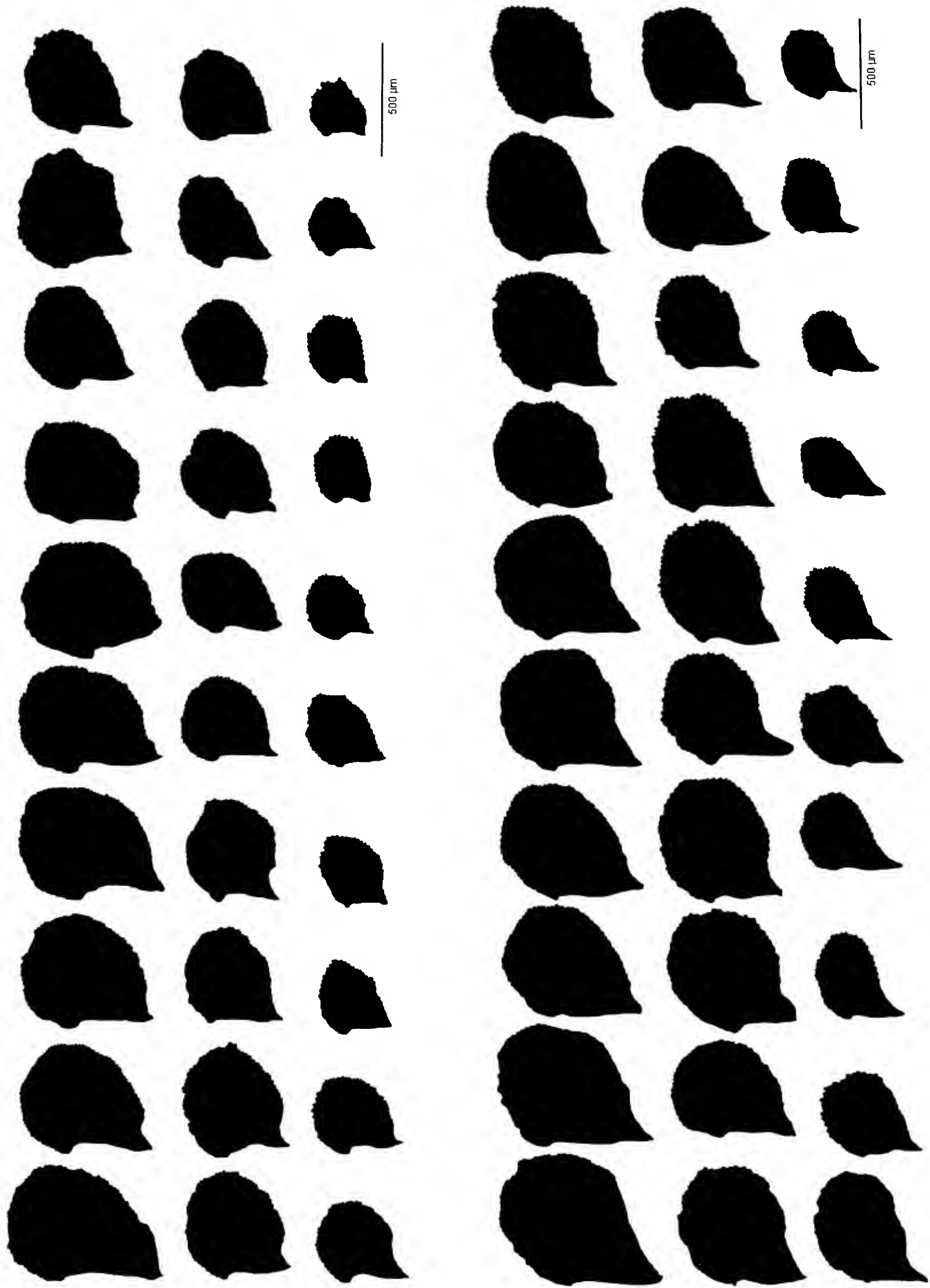


FIG. 6. Silhouettes of lateral leaves from the type collection of *Mnioloma stamatotomum* from Mt. Lewis, Queensland, Australia (upper 30 leaves; Renner 2139, NSW), and a collection from Mt. Kouakoué, New Caledonia (lower 30 leaves; Brown, NSW 760138).

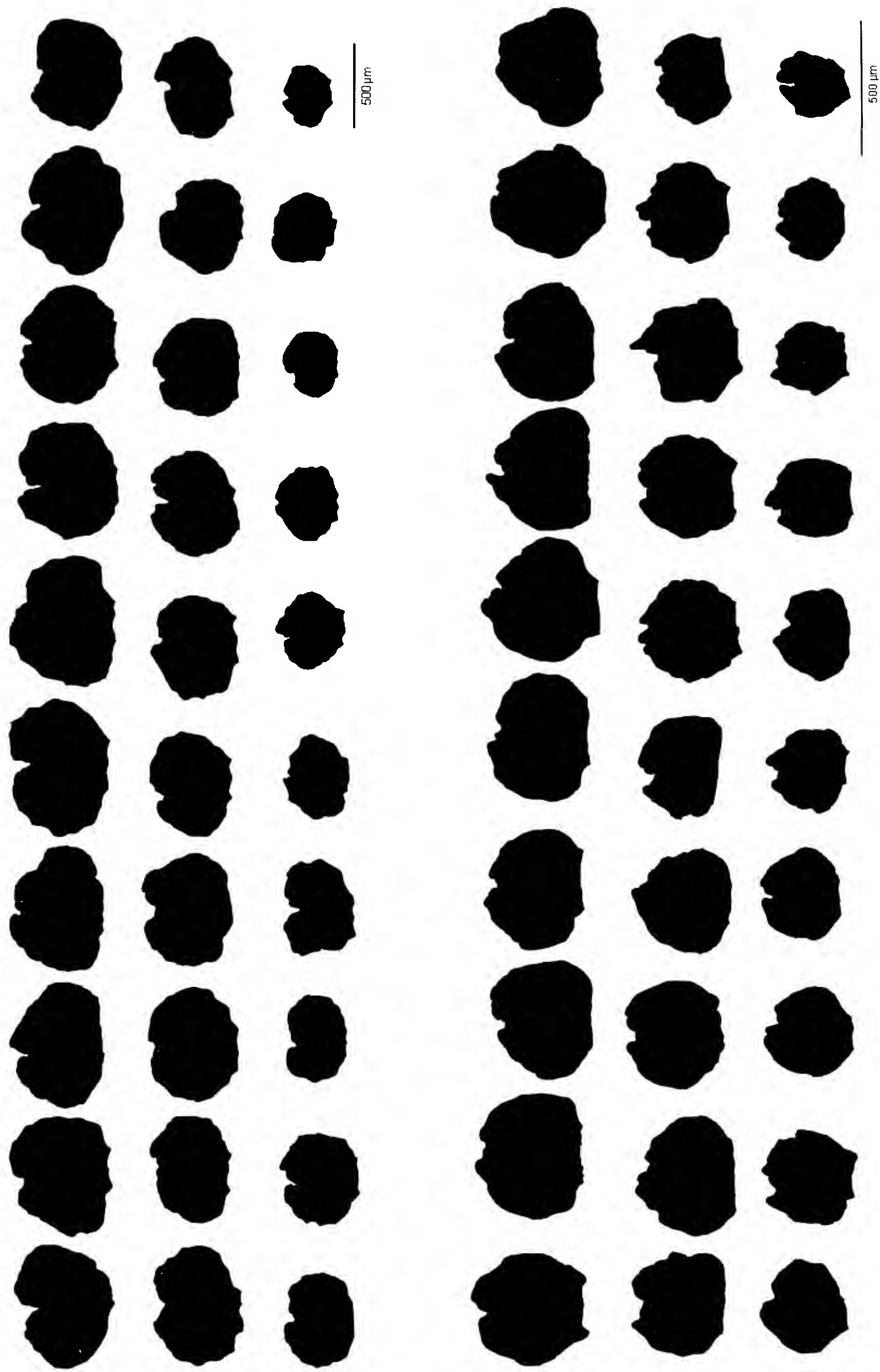


FIG. 7. Silhouettes of underleaves from the type collection of *Mnioloma novaezelandiae* (upper 30 underleaves; Renner CMS 1156 T/10, CHR) from Fiordland, New Zealand, and *M. cf. fuscum* (lower 30 underleaves) from Bartle Frere, Queensland, Australia (Renner 2219).

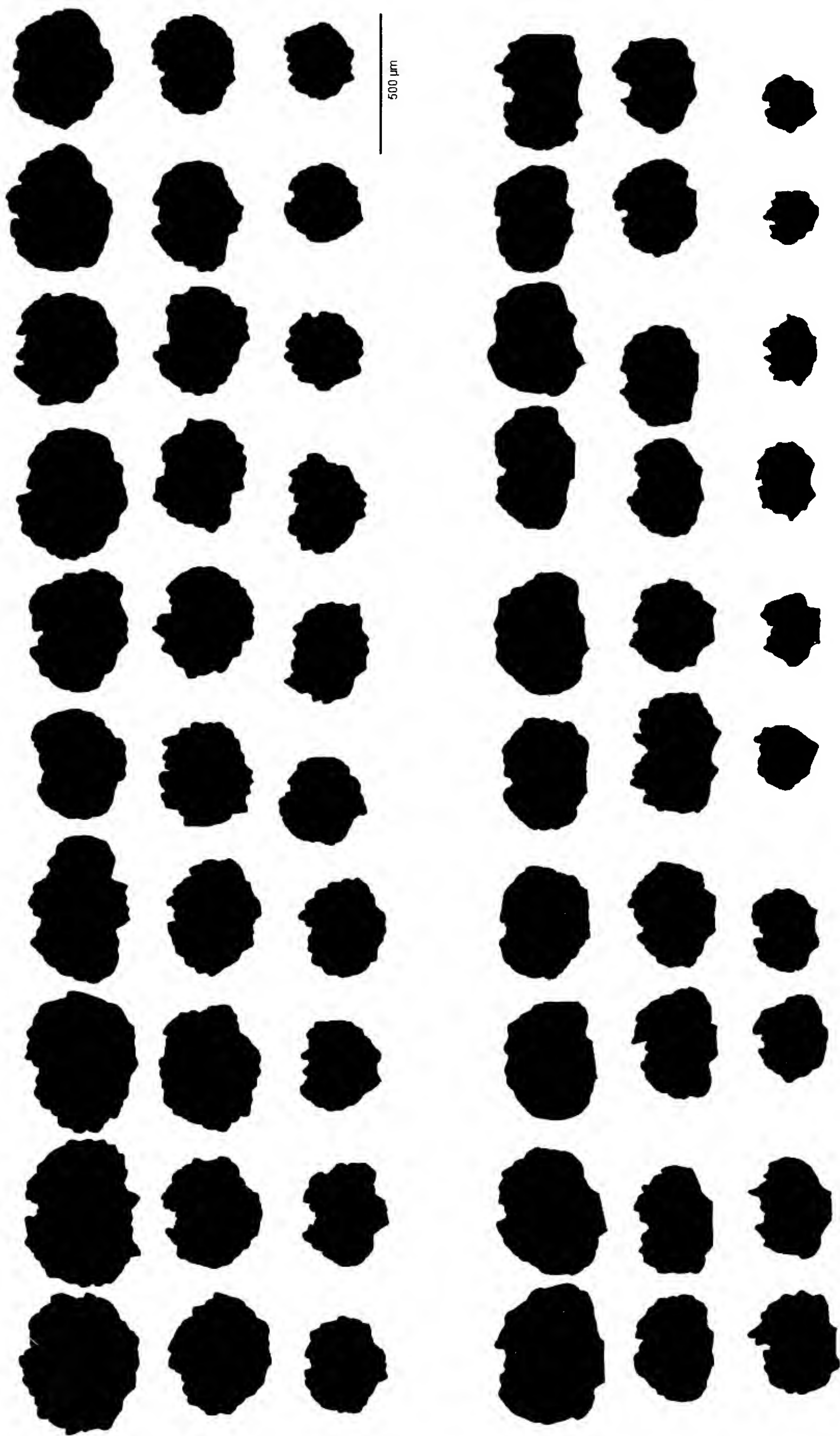


FIG. 8. Silhouettes of underleaves from the type collection of *Mnioloma stamatotomum* from Mt. Lewis, Queensland, Australia (upper 30 underleaves; Renner 2139, NSW), and a collection from Mt. Kouakoué, New Caledonia (lower 30 underleaves; Brown, NSW 760138).

and details of the marginal cells, e.g., in the monotypic subgenus *Mnioloma* the leaf margin is bordered by sinuous and strongly elongated cells that lie almost parallel with the margins and are contracted into a blunt beak at the leaf apex (Schuster, 2000). Schuster also refers (2000: 504) to intraspecific malleability, stating that it is “such that further synonymy is likely; the subgenus [*Caracoma*] needs careful study.”

The results of our examination of lateral and ventral leaves show that there are significant differences in the width of these features between all four specimens (although there is overlap in all measures). The isotype of *M. novaezelandiae* is statistically separable from the other three Australasian specimens using *post hoc* tests. Discriminant function analysis of shape can be used to classify our *a priori* groups with reasonable, but not outstanding, success.

On the basis of our statistical analysis, in combination with qualitative features of the leaf margin (in both the lateral and ventral leaves), we suggest that two species of *Mnioloma* are known from Australia, neither of which is *M. novaezelandiae*, contrary to Renner and Braggins (2006). One of these species differs from the types of *M. fuscum* and *M. novaezelandiae* in its crenulate leaf margins, lateral leaf shape, and irregularly crenate underleaf margins. This species also occurs in New Caledonia and is apparently novel. We present this species as new below. The other Australian plant differs from *M. novaezelandiae* in its leaf shape, which has the apex consistently squared (compare leaf outlines in Fig. 5) and is a smaller plant than *M. novaezelandiae*. This plant is comparable to *M. fuscum*, but again differs in leaf shape. It is known in Australia from two specimens, both from Mt. Bartle Frere, and we have been unable to clarify its relationship to any known species through our analysis. We do not have sufficient evidence to reject the inclusion of these plants within *M. fuscum*, nor to corroborate a hypothesis of difference. We acknowledge this uncertainty by presenting the plant as *Mnioloma* cf. *fuscum*, which we suggest be applied to these, and to other Australian material, until relationships of this plant can be clarified.

Mnioloma novaezelandiae is known from four specimens, ranging from Fiordland (South Island) to the Coromandel Peninsula (North Island). These specimens exhibit a number of differences from one another; in particular, the northern

plants have smaller underleaves with different marginal morphology and are slightly smaller than the Fiordland material, which is the type. This variability may be attributable to clinal variation, and if so, is worth quantifying as clinal variation is known in very few liverwort species. Few studies explicitly targeted at quantifying geographical patterns of morphological variation have been conducted within the Hepaticae (i.e., Therrien et al., 1998). Elucidation of morphological variation within the New Zealand *Mnioloma* would also inform grouping decisions we have made here. (Our intention was to include additional specimens of *M. novaezelandiae* in our analysis; however, time constraints and material availability mean that these specimens will be used in future analyses.)

Plasticity of the hepatic gametophyte, even within a single stem (Fig. 11.1), is well documented (e.g., Szweykowski, 1984; Mishler, 1988; Schuster, 2000). Mishler (1988) observed that “most leafy bryophytes produce a prolonged sequence of juvenile leaves before mature leaves characteristic of the species are developed” and that “rates of development can vary extraordinarily under simple and natural variation in light, temperature, and water relationships.” Future directions in multivariate analysis may be required to focus, not on the full range of variation, but on the form of mature leaves and/or plants grown in a series of different environments (Szweykowski, 1984) plus a wider range of characters (and specimens). Ultimately, the solution may be found only on recourse to DNA techniques.

Taxonomic Treatment

Mnioloma cf. *fuscum* (Lehm.) R. M. Schust.

Jungermannia fusca Lehm., Linnaea 4: 360. 1829; *Calypogeia fusca* (Lehm.) Steph., Spec. Hep. 3: 398. 1908; *Metacalypogeia fusca* (Lehm.) N. Kitag., Beih. Nova Hedwigia 90: 168. 1968. Type: South Africa, Cape Province, Tafelberg, *Ecklon s.n.* (s!).

(Description based on Australian material.) Plants procumbent/decumbent, fuscous (stems more so), small and delicate, leafy shoots mostly 730–1075 μm wide, corticolous in scattered patches amongst other bryophytes (Lejeuneaceae, *Bazzania*, etc.); branching very occasional (only

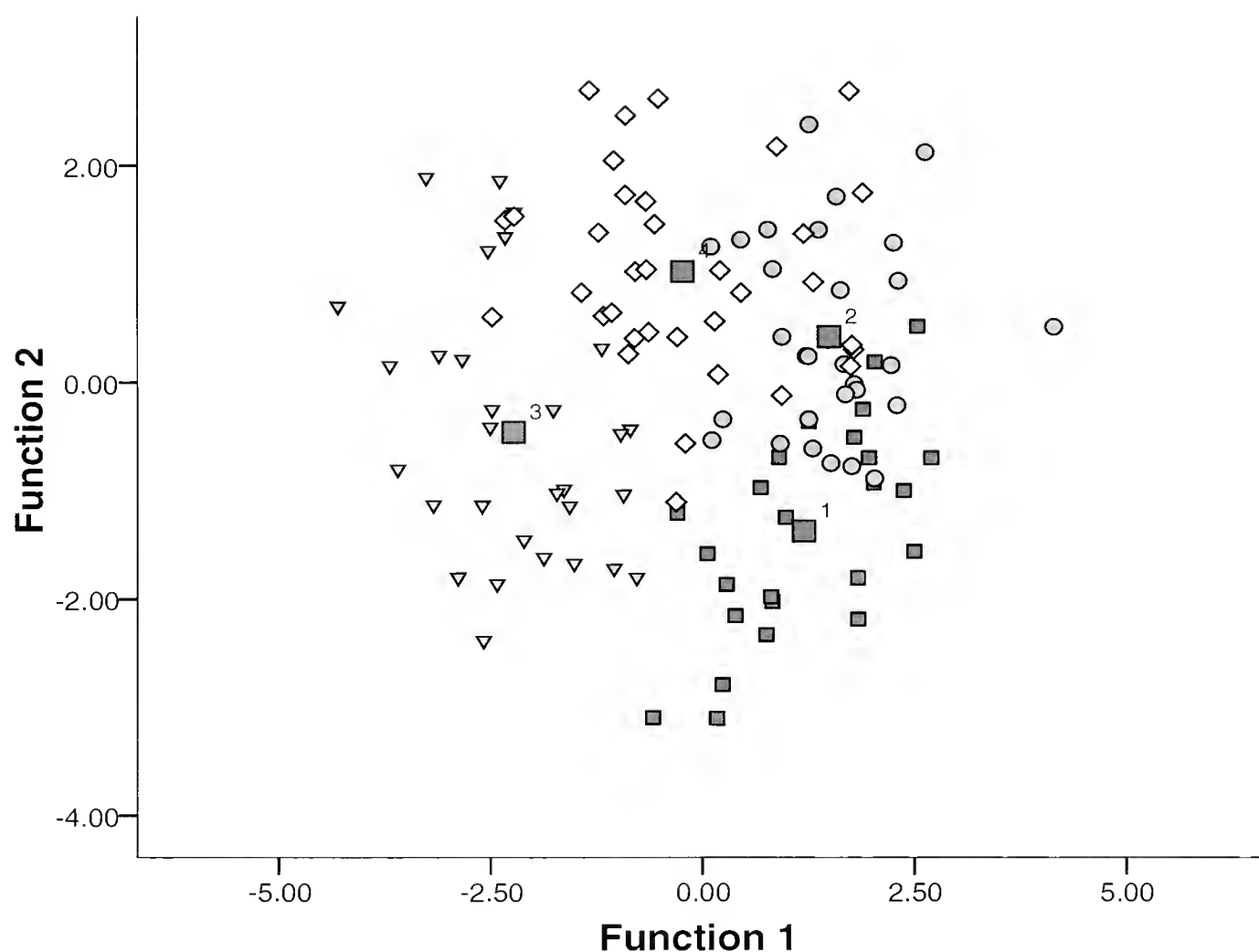


FIG. 9. Discriminant function analysis of principal components explaining variation in lateral leaf and underleaf shape for four specimens of *Mnioloma*. • = Bartle Frere. ■ = Fiordland. ▼ = Mt. Lewis. ◇ = Mt. Kouakoué. Large squares = centroids.

two sighted), ventral-intercalary, arising from the underleaf axil, with one or two smaller leaves initially, followed by normal leaves. Stems delicate, elliptical in cross section, ca. 100–115 μm wide and five or six cells high; cortical cells of similar size to medullary ones but with slightly thickened brownish walls, ca. 35–75 \times 13–20 μm (ventral slightly smaller, 25–70 \times 15–25 μm) in surface view, somewhat striolate. Rhizoids variable in expression, absent from some stems through to produced extensively on all but the youngest underleaf bases, in ill-defined fascicles, apices often dendritic. Leaves \pm flat, weakly imbricate to somewhat distant, dorsal insertion to midline, angle of insertion deviating shallowly from the vertical, widely spreading to somewhat oblique, rounded-quadrate to almost oblong with apices rounded to truncate or retuse, ventral base usually slightly decurrent, 330–420 μm long (from axis to apex of leaf) \times 234–330 μm wide; margin entire or sporadically irregular from protruding cells (tending to occur more frequently on certain shoots); marginal cells ca. 19–37 \times 14–21 μm (or somewhat wider when projecting, 17–22 \times 18–25 μm), smaller than cells towards center but grading into one another so a marginal border is not obvious, isodiametric to rectangular; central cells ca. 30–51 \times 20–37

μm , isodiametric to more usually rectangular/elongate polygonal (l:w < 2); cell walls mostly ca. 2 μm thick, often with ill-defined trigones, strongly verruculose. Underleaves 1.3–2 \times as broad as stem, inserted on (3)4–6 rows of stem cells, flat to feebly concave, remote, sub-orbicular, often apically notched, 110–210 μm long, (135)165–260 μm wide, margin almost entire to bluntly crenate/toothed; apical notches each with a slime papilla which is rapidly lost as underleaf matures; cells isodiametric to rectangular/elongate polygonal (mostly towards center of leaf), strongly verruculose. Oil-bodies not known. Asexual reproduction not observed. Reproductive features unknown. Figure 10.

DIFFERENTIATION AND VARIATION—Differing from *M. fuscum* primarily in the form of the underleaves which are more deeply lobed and irregular in outline (Fig. 7). This taxon does not appear to possess the small tooth on the dorsal base of the lateral leaf referred to by Engel (2006), but not all material in the scant type of *M. fuscum* displays this attribute. A few marginal cells on one young stem (Fig. 10.7) showed slight crenation of the lateral leaf margin. This feature has also been reported in the African populations of *M. fuscum* (Pócs, 2005). One stem of the Mt. Kouakoué specimen approached this material in

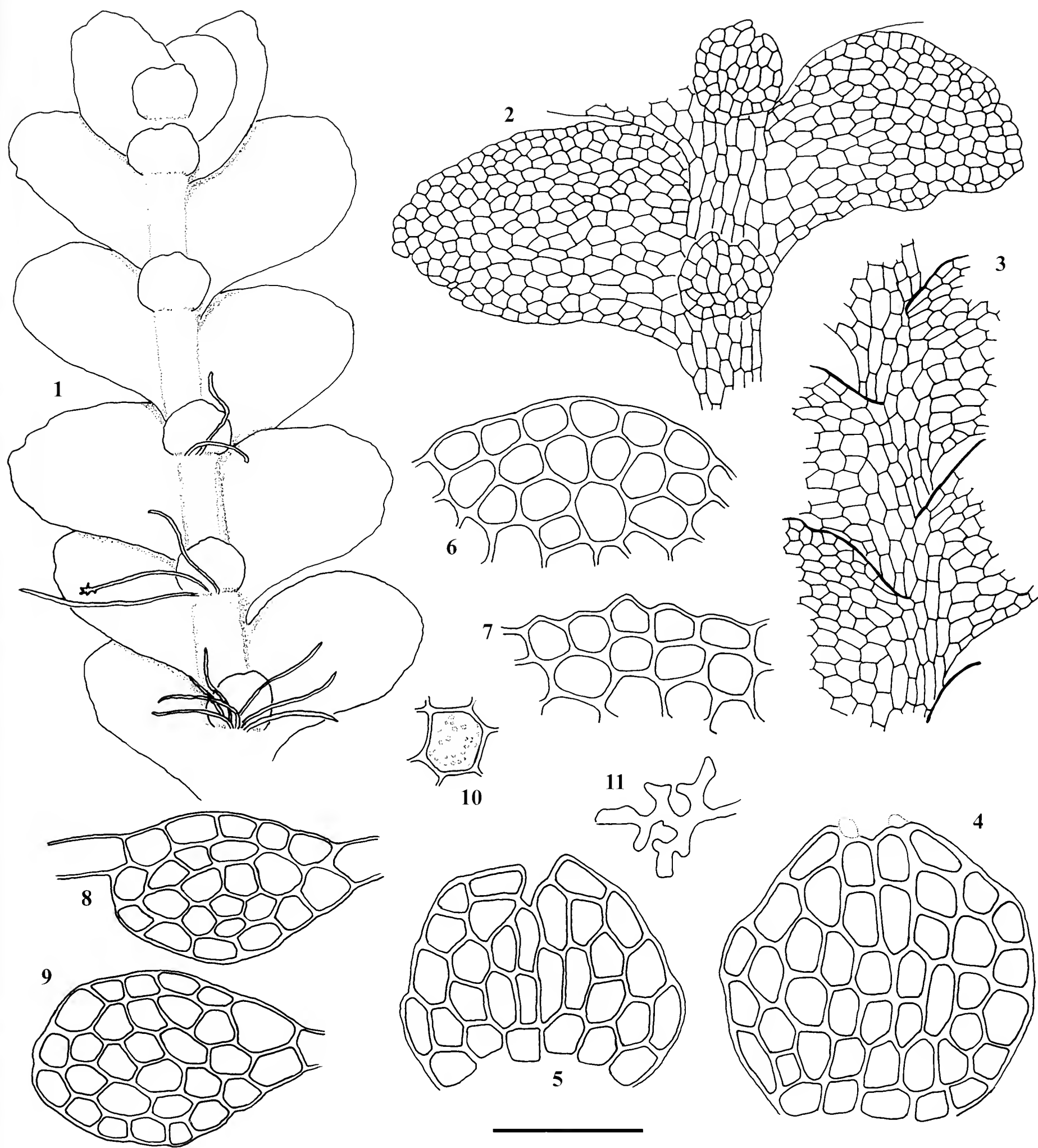


FIG. 10. *Mnioloma* cf. *fuscum* (Lehm.) R. M. Schust. (1) Plant, ventral view. (2) Portion of main stem, ventral view. (3) Portion of main stem, dorsal view, showing insertion of leaf bases to midline. (4, 5) Underleaves. (6, 7) Margin of lateral leaves, showing normal entire outline (6) or slight formation of crenations (7, rare). (8, 9) Stem, cross sections. (10) Lateral leaf cell showing cuticular detail. (11) Rhizoid, dendritic tip. Scale bar: 1 = 800 μ m; 2, 3 = 400 μ m; 4-9 = 200 μ m; 10, 11 = 130 μ m. (All from Renner 2219, Bartle Frere, Queensland, Australia.)

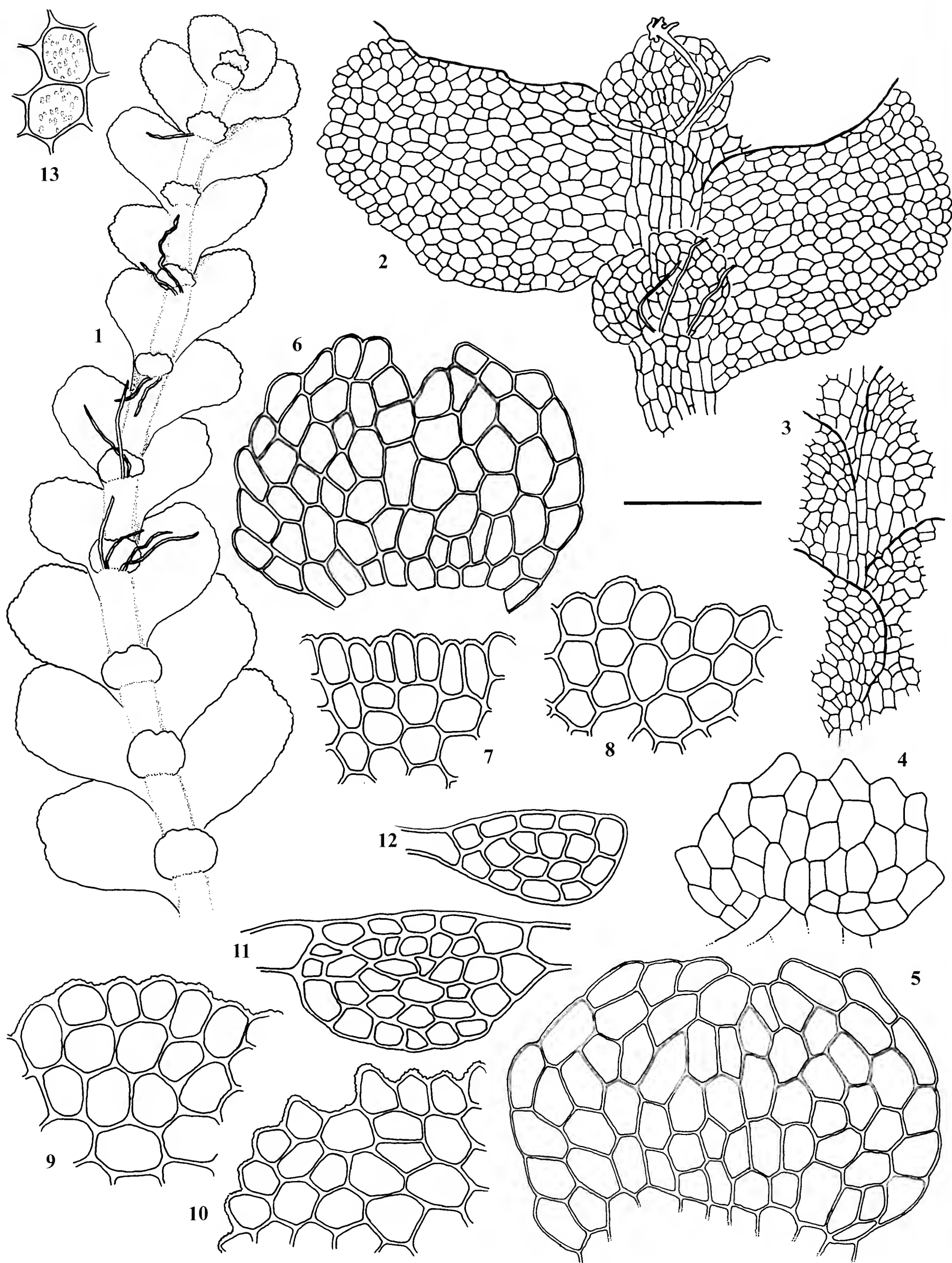


FIG. 11. *Mnioloma stamatotonum* M. A. M. Renner & E. A. Br. (1) Plant, ventral view. (2) Portion of main stem, ventral view. (3) Portion of main stem, dorsal view, showing insertion of leaf bases to midline. (4-6) Underleaves. (7-10) Margin of lateral leaves, showing variation in crenations. (11, 12) Stem, cross sections. (13) Lateral leaf cell showing cuticular detail. Scale bar: 1 = 800 μm ; 2, 3 = 400 μm ; 4-12 = 200 μm ; 13 = 130 μm . (2, 3, 6-8, 12, 13 from Renner 2139, Mt. Lewis, Queensland, Australia; 1, 4, 5, 9-11 from Brown NSW 760138, Mt. Kouakoué, New Caledonia.)

degree of crenation, but each cell of the margin was slightly protruding (versus a few scattered cells in the Bartle Frere material) and the cuticle was heavily verrucose. The underleaves are inserted on 3–6 rows of stem cells (versus the 8–13 reported for *M. fuscum*; but similarly this feature is variable in the type material with some leaves apparently inserted on as few as five stem cells). More material of *M. fuscum* needs to be investigated before the identity of this taxon can be ascertained with confidence.

DISTRIBUTION AND ECOLOGY—Known in Australia only from two collections from the western face of Bartle Frere in the Wet Tropics of Queensland. Specimens were found growing amongst luxuriant bryophyte mats on the rotten base of a still living tree in riparian forest and epiphytically amongst dense bryophytes on tree trunks. In both situations they were growing in bright but filtered light.

SPECIMENS SEEN—**Australia. Queensland:** Wooroonooran National Park, Bartle Frere, *Brown & Renner* (NSW 760045); *ibid.*, *Renner 2219* (NSW 760046).

Mnioloma stamatotonum M. A. M. Renner & E. A. Br., **sp. nov.**

Folia verruculosa rotundo-quadrata, basi aliquantum decurrentia, ad lineam mediam dorsaliter inserta, apicibus rotundatis, marginibus propter cellulas protrusas valde crenatis. Amphigastria in (4)5–7 seriebus cellularum caulinarum inserta, marginibus plerumque obtuse dentatis raro subintegris.

Holotype: Australia, Queensland, Mt. Lewis, *M.A.M. Renner 2139* (NSW 760047); **isotypes** (F, P).

Plants procumbent to decumbent, fuscous (stems more so), small and delicate, leafy shoots mostly 580–900 μm wide, corticolous in scattered patches amongst other bryophytes; branching very occasional (usually below damaged apices), ventral-intercalary, arising from the underleaf axil, with one or two smaller leaves initially, followed by normal leaves. Stems delicate, elliptical in cross section, ca. 90–125 μm wide and 4–6 cells high; cortical cells of similar size to medullary ones but with slightly thickened brownish walls, ca. 25–70 \times 10–30 μm (ventral slightly smaller, 20–45 \times 10–20 μm) in surface view, somewhat striolate. Rhizoids variable in expression, absent from some stems through to produced extensively on all but the youngest

underleaf bases, in ill-defined fascicles, apices often dendritic. Leaves \pm flat, imbricate to somewhat distant (particularly on younger stems), dorsal insertion to midline (or sometimes with a one-cell or partially two-cell free strip in New Caledonian material), angle of insertion deviating shallowly from the vertical, widely spreading (normally almost at 90° to stem) to somewhat oblique, rounded-quadrate with apices rounded, ventral base usually slightly decurrent, 240–570 μm long \times 230–540 μm wide; apical and antical margin strongly crenate from protruding cells; marginal cells ca. 21–31 \times 9–22 μm , isodiametric to rectangular with up to half of cell projecting beyond the margin, slightly smaller than cells towards base of leaf but grading into them and not forming a distinct border; central cells ca. 19–50 \times 19–24 μm , isodiametric to more usually rectangular/elongate polygonal (l:w typically ca. 1.5); cell walls mostly ca. 1 μm thick, rarely with slight thickening at cell junctions, strongly verrucose, projecting portion of marginal cells frequently thickened, ca. 2 μm thick. Underleaves 1.3–1.9 \times as broad as stem, inserted on (4)5–7 rows of stem cells, flat to feebly concave, remote, suborbicular to more usually somewhat oblong, usually shallowly apically notched, 90–190 μm long, 100–265 μm wide, margin rarely almost entire to bluntly crenate/toothed; apical notches each with a slime papilla which is rapidly lost as underleaf matures; cells isodiametric to rectangular/elongate polygonal, strongly verrucose. Oil-bodies not known. Asexual reproduction not observed. Reproductive features unknown. Figure 11.

DIFFERENTIATION AND VARIATION—Differing from other species of *Mnioloma* in Australasia in the crenulate leaf margins, the distal half of the lamina nearly circular, and the sculpted underleaf margins (Figs. 7, 8, 11).

DISTRIBUTION AND ECOLOGY—Known from one collection from Australia and one specimen from New Caledonia. In Australia this species grew scattered through other bryophytes growing epiphytically on the trunk of a tree within tropical submontane rainforest on Mt. Lewis. One of the co-occurring species was *Lejeunea patersonii* (Steph.) Steph., currently considered a New Caledonian endemic. In New Caledonia the habitat is similar, differing only in the species making up the forest and the bryophytes that it grew amongst.

ETYMOLOGY—The words used to construct this name have their roots in the Greek language

(τραυλός—stammer and φωνή—voice) but the result is quite deliberately artificial. It is a light-hearted reference to the many names in hepaticology that on utterance cause one to pause and/or stutter.

SPECIMENS SEEN—**New Caledonia:** Mt. Kouakoué, E.A. Brown (NSW 760138).

Acknowledgments

The Kouakoué specimen was collected while participating in a botanical inventory of the mountain, supported by National Geographic Society (Grant N°7579-04) and the South Province of New Caledonia; Dr. Jérôme Munzinger of IRD, Noumea, led the expedition and E.A.B. is indebted to him for his assistance and kindness. We wish to thank the following institutions for the loan of specimens—AKU, CHR, F, S—and the Queensland Government for allowing us access to their national parks. The support and encouragement of research in the Wet Tropics by Andi Cairns is appreciated and was partially supported by the Hermon Slade Foundation (for work on the Lepidoziaceae).

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FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Six: Liverwort Floristics and Revisions—Asia and Australasia

Chapter Fifteen: A new *Bazzania* species (Lepidoziaceae) from Stockton Plateau, Nelson, South Island, New Zealand

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Abstract

A new species, *Bazzania engelii*, is described from two sites on Stockton Plateau, a sloping plateau between 200 and 1100 m asl northeast of Westport, South Island, New Zealand. *Bazzania engelii* is compared with other New Zealand *Bazzania* species but is not placed in a subgenus. The species has a superficial similarity to *B. nitida*, but the frequent production of ventral-intercalary branches with normal leaves suggests a relationship with *B. exempta*.

Introduction

The genus *Bazzania* Gray is a very large, worldwide genus, with most species in the tropics and Southern Hemisphere; it has never been monographed. Schuster (2000) states that

Stephani's 4 subgenera and 11 sections are to a large extent artificial, and that the taxonomy of the group needs methods other than those used previously to elucidate the relationships of the species.

Ten species are recognized as being in New Zealand, including three newly described in the last 15 years: *Bazzania nova* J.J.Engel & Merr. (Engel & Merrill, 1994), *B. exempta* J.J.Engel (Engel, 2006), and *B. okaritana* Meagher & Glenny (Meagher & Glenny, 2007), and one, *B. accreta* (Lehm. & Lindenb.) Trevis., an Australian species newly recognized as being in New Zealand (Meagher, 2003).

A new species has been found this year, at two sites on Stockton Plateau. The name honors John Engel, who has added to our knowledge of *Bazzania* in New Zealand through three papers (Engel & Schuster, 1988; Engel & Merrill, 1994; Engel, 2006) that were the first new contributions on *Bazzania* in New Zealand since Hodgson's work of 1954 (Hodgson, 1954), as well as major contributions to our understanding of the family Lepidoziaceae in Australasia (e.g., Engel & Merrill, 2004).

Taxonomy

Bazzania engelii Glenny, sp. nov.

Planta erecta, ramis aequae ventraliter intercalaribus et frullanioidibus. Folia non caduca, opposita, subvittata, asymmetrice ovata, apicibus 3-dentatis. Amphigastria rectangularia, foliis 2-connatis, apicibus intergerrimis, cellulis chlorophyllosis. Cellulae vittatae foliales trigonis parvis sed trigonae nullae in cellulis nonvittatis. Androecia et gynoecia desunt.

HOLOTYPE: New Zealand, South Island, Western Nelson Ecological Province, Stockton Plateau, Manganui Stream, Weka Stream, NZMS 260 L28 193533, 240 m, *R. Bartlett* s. n., 27 March 2007, CHR 592014. Isotypes: AK, F. (Fig. 1A–J).

Plants erect, small, 15–20 mm long, yellow- to olive-green when fresh, plants blackish green when dry; leaves not membranous; shoots to 2.1 mm wide. Branching frequent, leafy branches mostly of the *Frullania* type, pseudodichotomous with branch lengths equal. Branch half-leaf symmetric, ovate, undivided, non-vittate, the apex acuminate, auriculate at the base, cells at median base weakly trigonous and rectangular. First branch underleaf unequally 3-lobed, the deepest sinus 0.4× that of the underleaf, transversely inserted on ventral-lateral side of juncture of main axis and branch, free from and juxtaposed to, or narrowly joined to the underleaf

of the main axis. Ventral-intercalary branches frequent, of two types, branches with normal leaves much less abundant than geotropic branches with microphylls. Stem ca. 300 µm diam., slightly flattened, cells uniformly thick walled (3 µm thick). Rhizoids not seen. Leaves opposite, strongly incubous, slightly imbricate, the ampliate acroscopic leaf bases covering most of the stem in dorsal view, widely spreading (ca. 90°), slightly convex, the apex strongly incurved; 1100–1300 mm long, 750–950 mm wide, asymmetrically ovate; apex broadly rounded to often obliquely truncate, with (2–)3(–4) small, sometimes obscure teeth; the teeth typically 2 cells wide at base, composed of only 1–4 cells, the apex otherwise entire; dorsal margin strongly ampliate and auriculate, extending beyond the middle of the stem, entire, not decurrent; ventral margin straight or slightly ampliate at the base and concavely arching in the upper two-thirds, entire, not decurrent. Vitta of leaves indistinct, ca. 7–9 cell rows wide at midleaf; parallel to, and 4–7 cells within the ventral margin at midpoint of leaf; cells of vitta base rectangular, 27–70 µm long, 22–40 µm wide, weakly trigonous. Non-vittate cells at widest part of leaf isodiametric to rectangular, 13–22 µm long × 13–15 µm wide, walls ca. 2.5–3.0 µm thick, trigones absent; cells below the apex almost isodiametric, 14–23 × 14–18 µm; both leaf surfaces smooth. Outer five rows of cells on the acroscopic margin hyaline. Oil-bodies present in some distal cells of both margins, absent from the marginal cell row on the basisopic margin, absent from the seven outer cell rows on the acroscopic margin; colorless, largest, and most numerous in cells at the base of the vitta and there (2–)3–5(–8) per cell, irregularly ellipsoidal, not platelet-like, homogeneous, smooth or (in larger ones) with dimples or weak folds or constrictions, which lend a potato-like aspect to the shape, 6–13.5 µm long × 5–9 µm wide; oil-bodies of non-vittate cells similar to those of the vitta but much smaller and 1–3 per cell, those at leaf apex 2–7 µm long × 2–4 µm wide, the smallest ones smooth without any surface markings, the larger ones with dimples and folds as in the vitta oil-bodies. Underleaves wider than the stem, at ca. 60° to the stem, distant, connate to lateral leaves on both sides, the bridging tissue five cells wide; slightly convex, not membranous, wider than long, 500–530 mm long × 600–700 mm wide; apex recurved, ± rectangular, apex and outer margins very weakly lobed/

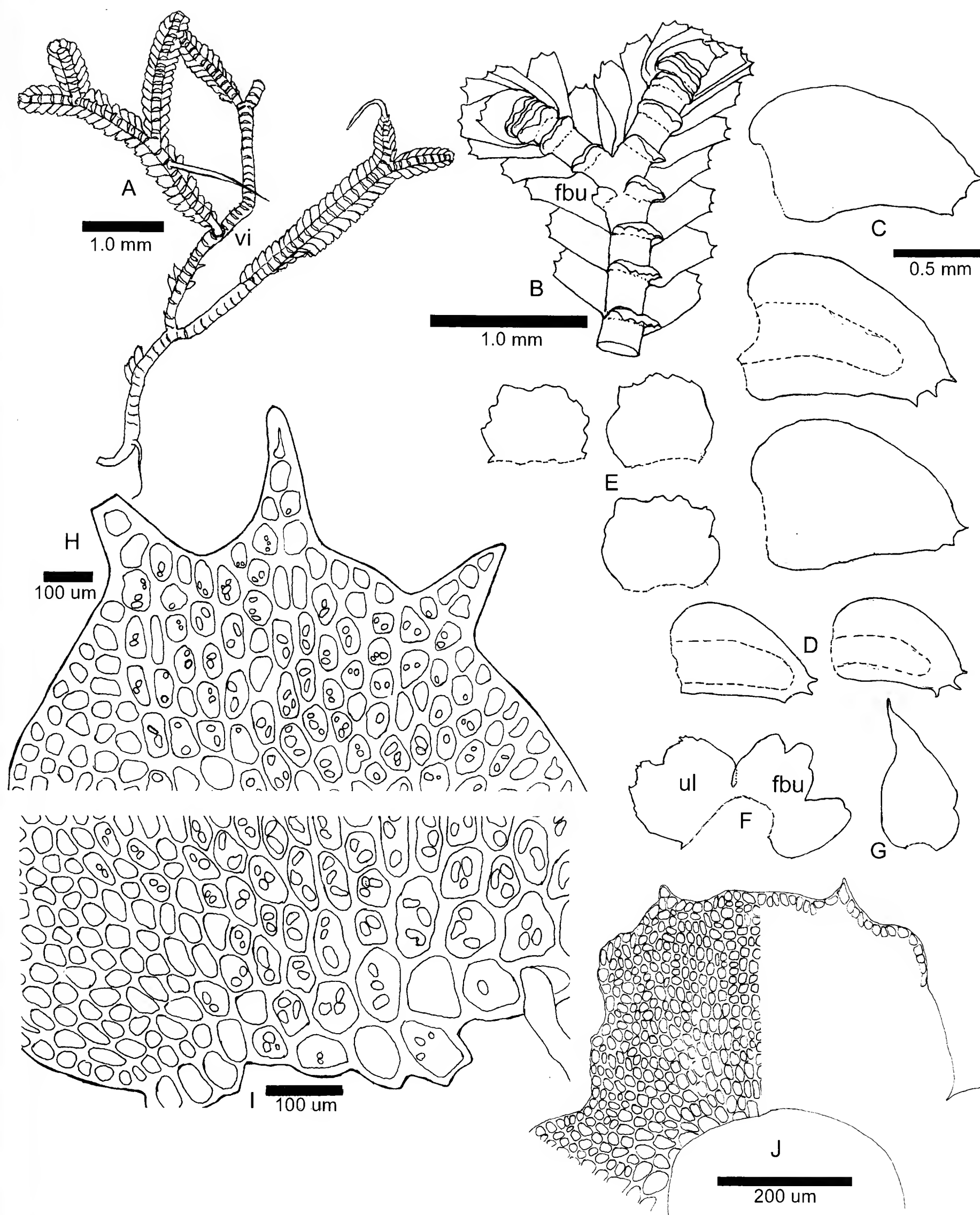


FIG. 1. *Bazzania engelii*. (A) Whole plant, ventral view, showing one ventral-intercalary branch with normal leaves (= vi), one ventral-intercalary microphyllous branch, the others terminal. (B) Terminal branch showing position of first branch underleaf (= fbu), free from the adjacent normal underleaf in this case. (C) Lateral leaves on main shoot; zone of vitta cells enclosed by dashed line. (D) Lateral leaves on a smaller, younger branch; zone of vitta cells enclosed by dashed line. (E) Underleaves. (F) Asymmetrically lobed first branch underleaf (= fbu) connate to a normal underleaf (= ul). (G) Branch half-leaf. (H) Leaf apex. (I) Leaf base. (J) Underleaf; right half shows single incomplete marginal row of hyaline cells. All illustrated from the holotype.



FIG. 2. Type locality of *Bazzania engelii* in Weka Stream, Stockton Plateau.

toothed, sinus depth $0.07 \times$ the length of the underleaf, the lobes/teeth entire. Underleaf cells chlorophyllose throughout or with 1–2 rows of cells forming a hyaline border in the distal half of the leaf; cells \pm isodiametric, thick-walled ($4 \mu\text{m}$ thick), those at the median base ca. $25 \mu\text{m}$ wide and long, trigones weak, rhizoids not seen; surfaces smooth. Asexual reproduction by caducous leaves completely absent. Gynoecia and androecia unknown.

HABITAT—Names of plants that follow are in accordance with the New Zealand Plant Names Database, <http://nzflora.landcareresearch.co.nz/>. Weka Stream at the type locality (Fig. 2) flows across sandstone bedrock. The upper gully banks are gently sloping (approx. 15°), with a shrubby cover 0.5–2 m high of *Gleichenia dicarpa*, *G. microphylla*, *Blechnum novae-zelandiae*, *Leptospermum scoparium*, and *Phormium cookianum* with *Coprosma robusta*, *Dracophyllum longifolium*, *Gahnia procera*, *Weinmannia racemosa*, *Dacrydium cupressinum*, and *Metrosideros umbellata*. The ground layer includes *Empodisma minus*,

Lycopodiella diffusa, small saplings of *Podocarpus hallii* and *Lepidothamnus intermedius*, and some *Lepidosperma australe*. On steeper banks, trees of *Dacrydium cupressinum*, *Pseudopanax crasifolium*, *Phyllocladus alpinus*, and *Nothofagus solandri* var. *cliffortioides* approximately 8 m high shade the riparian margins, with occasional *Dacrydium cupressinum* extending above this canopy. Bryophyte cover along the riparian margins is almost continuous, with occasional *Blechnum novaezelandiae* and *Phormium cookianum* trailing over the banks.

Bazzania engelii was growing in sandy stream-deposited soil, erect through cushions of mainly *Campylopus clavatus*, *Dicranoloma robustum*, and *Wijkia extenuata*, with *Acromastigum colensoanum*, *Cryptochila grandiflora*, *Herbertus oldfieldianus*, *Hymenophyllum multifidum*, *Kurzia hippuroides*, *Lepicolea attenuata*, *Lepidozia kirkii*, *Pseudocephalozia paludicola*, *Rhizogonium pennatum*, *Riccardia cochleata*, *Siphula decumbens*, *Zoopsis argentea*, and *Z. setulosa*.

At a second site in Herbert Stream, *Bazzania engelii* was collected with epiphytes such as *Lepicolea scolopendra* and *Paraschistochila tuloides*, but was on humus, so it appears it may have been collected near the base of a tree, or around roots, an intermediate situation between terrestrial and epiphytic environments.

OTHER SPECIMENS SEEN—Stockton Plateau, near head of Herbert Stream, NZMS 260 L29 150441, 860 m, “bank sample, partial canopy” (litter contains *Nothofagus solandri* var. *cliffortioides* and *Halocarpus biformis*), associated with *Bunodophoron australe*, *Herbertus oldfieldianus*, *Heteroscyphus menziesii*, *Hymenophyllum armstrongii*, *Lepicolea scolopendra*, *Metzgeria scobina*, and *Paraschistochila tuloides*; J. Hughes s. n., 21 June 2007, CHR 592013, AK.

Differentiation

Bazzania engelii is superficially similar to *B. nitida* (Web.) Grolle. It shares with *B. nitida* ovate, concave leaves with small, indistinct teeth at the narrow leaf apex, which is recurved and not visible in dorsal view. However, it differs in important respects: the leaves are opposite (alternate in *B. nitida*), the underleaves are hardly lobed or toothed (deeply lobed in *B. nitida*), and the vitta is indistinct (distinct in *B. nitida*).

An unusual feature of *B. engelii* is that ventral-intercalary branches with normal leaves are abundant. Unbiased samples of plants were measured to determine the ratio of terminal to leafy ventral-intercalary branches. In one sample removed from the type, of 30 branchings 18 were terminal and 12 were leafy ventral-intercalary. In a second clump of material in the type, ventral-intercalary branches with microphylls were also measured. Of 76 branchings, 31 were terminal, 38 were microphyllous-ventral-intercalary, and 7 were leafy ventral-intercalary. In the Herbert Stream specimen, of 85 branchings, 28 were terminal, 53 were microphyllous ventral-intercalary, and 4 were leafy ventral-intercalary. In these three samples, the ratio of leafy ventral-intercalary branches to terminal branches was 0.40, 0.18, and 0.14, respectively. This suggests that the proportion of branching types is not fixed, and it may be influenced by microhabitat. Perhaps the production of leafy ventral-intercalary branches is a response to burial by stream silt.

Bazzania exempta (Engel, 2006) has almost exclusively ventral-intercalary leafy branches (only one *Frullania*-type branch was seen in the type), while other species in New Zealand have only occasional leafy ventral-intercalary branches. For this reason, *B. exempta* was placed in its own section, sect. *Exemptae* J.J.Engel. *Bazzania exempta* otherwise most resembles *B. hochstetteri* (Reichardt) E.A.Hodgs. and *B. okaritana* in having narrowly rectangular leaves, whereas *B. engelii* has ovate leaves that are ampliate at the acroscopic base. The underleaves are either completely chlorophyllose or with a narrow hyaline border, a feature shared with *B. nova* and *B. okaritana*. The underleaves resemble those of *B. okaritana* in being almost entire, but are wider than long (quadrate in *B. okaritana*).

The frequency of ventral-intercalary leafy branches in *B. exempta* and *B. engelii* and the shared stream bank habitat suggests these two species should be compared most carefully (Table 1). Even if with further material, the two species were found to overlap in frequency of the different branching types, the other differences tabled are sufficient to maintain them as distinct species.

The lateral leaf apices are entire, although 3-lobed, whereas *B. adnexa* (Lehm. & Lindenb.) Trevis. and *B. involuta* (Mont.) Kuntze have fine teeth at their leaf apices, suggesting that *B. engelii* is not closely related to either of those two species.

In summary, *B. engelii* shares features with a number of New Zealand species, but apart from being a member of the group of species that has opposite leaves (*B. accreta*, *B. adnexa*, *B. exempta*, *B. hochstetteri*, *B. involuta*, *B. nova*, *B. novaezelandiae* (Mitt.) Besch. & C.Massal., and *B. okaritana*), it is not possible to say which species in that group it most resembles.

Bazzania engelii is not known from Australia (D. Meagher, pers. comm.).

Distribution and Conservation Status

Bazzania engelii is known only from two localities 8 km apart on Stockton Plateau. Further field work is needed to establish its range, but the area of Stockton Plateau has been intensively surveyed for bryophytes over the last five years so it appears not to be common there. In the threat classification scheme of Molloy et al. (2001), its threat status should be “Nationally Critical” with the qualifier “Data Poor.”

TABLE 1. Differences between *Bazzania engelii* and *B. exempta*.

	<i>B. engelii</i>	<i>B. exempta</i>
Terminal branching	predominant	very rare (one seen)
Leaf permanence	never caducous	frequently caducous
Leaf width (µm)	750–950	400–450
Dorsal margin of leaf	strongly ampliate	not ampliate to moderately ampliate
Subvitta width at midleaf	occupying about half of leaf width	occupying most of leaf width
Underleaf connation with lateral leaves	connate both sides	free both sides
Underleaf hyaline zone	absent or 1–2 marginal cell rows	occupying lobes up to 0.35 depth of underleaf

Acknowledgments

This species was collected as part of work funded by Meridian Energy and by Solid Energy, on land that is part of Solid Energy’s mining concession and on land administered by the Department of Conservation. We thank those organizations for their assistance and especially Joseph Hughes of Solid Energy who collected the *Bazzania* at Herbert Stream. We thank David Meagher for his advice on the distinctness of the species. Thanks to Patricia Eckel and an anonymous reviewer for checking the Latin diagnosis, and to Allan Fife and Patrick Brownsey for comments on a draft.

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Abstract

An illustrated key to the currently accepted 10 species of *Porella* in North America north of Mexico is presented. The only known American locality of *P. gracillima* is described.

Introduction

Nine species of *Porella* L. are currently accepted for North America north of Mexico: *P. bolanderi* (Austin) Pearson, *P. cordaeana*

(Huebener) Moore, *P. fauriei* (Steph.). S. Hatt., *P. japonica* (Sande Lac.) Mitt., *P. navicularis* (Lehm. & Lindenb.) Pfeiff., *P. pinnata* L., *P. platyphylla* (L.) Pfeiff., *P. roellii* Steph., and *P. swartziana* (F. Weber) Trevis. (Schuster, 1980;

Hong, 1983; Piippo & Norris, 1996; Therrien et al., 1998; Hentschel et al., 2007). A further species, *P. wataugensis* (Sull.) M. Howe, was lowered to *P. pinnata* fo. *wataugensis* (Sull.) R. M. Schust. by Schuster (1980), supposing it to represent *P. pinnata* phenotypes with weakly toothed leaf margins. Simultaneously Schuster (1980) placed this taxon in the synonymy of *P. japonica*, whereas Hicks (1990) treated the taxon as a distinct species. For the time being, we accept Schuster's (1980) treatment of *P. wataugensis* as a local expression of *P. pinnata*.

In January 1992, a 10th species, *Porella gracillima* Mitt., was discovered for North America by the second author during bryological reconnaissance with Great Smoky Mountain National Park resource management personnel and University of Tennessee bryologists. North American material was initially identified as *P. urogea* C. Massal., and a specimen was sent to S. Hattori for confirmation. S. Hattori (in litt.) determined the specimen as *P. gracillima* subsp. *urogea* (C. Massal.) S. Hatt. & M. X. Zhang (Hattori & Zhang, 1985), but the discovery remained unpublished for 15 years. In 2007, finally, the North American population of *P. gracillima* subsp. *urogea* was included in a molecular phylogenetic study, and the range extension of the Asian taxon to North America was published (Hentschel et al., 2007).

Although the subject of several taxonomic studies, *Porella* has no synoptic key for North America. Here, we present an illustrated key to *Porella* in North America and describe the only known American locality of the Asian *P. gracillima*.

***Porella gracillima* in North America: Morphology, Distribution, and Habitat**

Porella gracillima is widespread in temperate Asia and has been recognized from Northwest India, China, Taiwan, the Altai Mountains, East Siberia, Sakhalin, and Japan (Hattori, 1969, 1971; Hattori & Zhang, 1985). In North America, *P. gracillima* appears to be restricted to a single locality in the southwest portion of the Great Smoky Mountains National Park, Blount County, Tennessee (the exact location is withheld to protect the population from exploitation by collectors).

Porella gracillima s. str. and *P. gracillima* subsp. *urogea* were separated from each other by the development of basal appendages of underleaves

and lobules (Hattori, 1971); however, this character is subject to variation in the various collections of the North American population. *Porella gracillima* s.l. is characterized by its small size, strongly involute entire lobes, and ciliate-undulate underleaf and lobule bases (Fig. 1). The North American population stands out by numerous plants developing two lobules per lobe (Fig. 1F). Except for the aberration of two lobules per lobe, the North American plants are well developed and frequently produce juvenile female inflorescences (perianths not developed). Male plants are unknown in North America.

In Tennessee, *P. gracillima* is restricted to two areas of karst topography separated by about 75 meters. Both areas are in a rich cove hardwood forest dominated by an overstory of *Tilia americana* var. *heterophylla* (Vent.) Loudon, *Acer saccharum* Marshall, *Liriodendron tulipifera* L., and *Tsuga canadensis* (L.) Carrière. The rock outcrops to which *P. gracillima* is limited are Jonesboro Limestone (Southworth et al., 2003). The larger of the two areas is approximately 160 square meters located on a NW-facing slope with numerous limestone outcrops that are no larger than 1 meter tall. The rich herbaceous ground layer consists of *Actaea pachypoda* Elliott, *Anemonella thalictroides* (L.) Spach, *Botrypus virginianus* (L.) Holub, *Delphinium tricornis* Michx., *Geranium maculatum* L., *Hybanthus concolor* (T. F. Forst.) Spreng., *Iris cristata* Aiton, *Laportea canadensis* (L.) Wedd., *Polymnia canadensis* L., *Sanguinaria canadensis* L., *Solidago flexicaulis* L., *Symphyotrichum cordifolium* (L.) Nesom, *Trillium luteum* (Muhl.) Harb., and *Uvularia perfoliata* L. Here, *P. gracillima* is locally common and occurs hanging in mats over the face of limestone, at soil level at the base of limestone, on ceilings directly on limestone, and over the moss *Anomodon rostratus* (Hedw.) Schimp. Other plants growing in close association on limestone with *P. gracillima* include *Brachythecium* sp., *Bryoandersonia illecebra* (Hedw.) H. Rob., *Rhodobryum ontariense* (Kindb.) Paris ex Kindb., and *Sedum ternatum* Michx. The second area is only about 25 square meters and is noticeably cooler than surrounding terrain because it is located on a streamlet where limestone outcrops rise to nearly 2 meters tall. The ground flora consists of *Cystopteris* sp., *Diplazium pycnocarpon* (Spreng.) M. Broun, *Hydrangea arborescens* L., *Hydrophyllum canadense* L., and *Ranunculus recurvatus* Poiret. Associated bryophytes on limestone include *Anomodon attenuatus* (Hedw.)

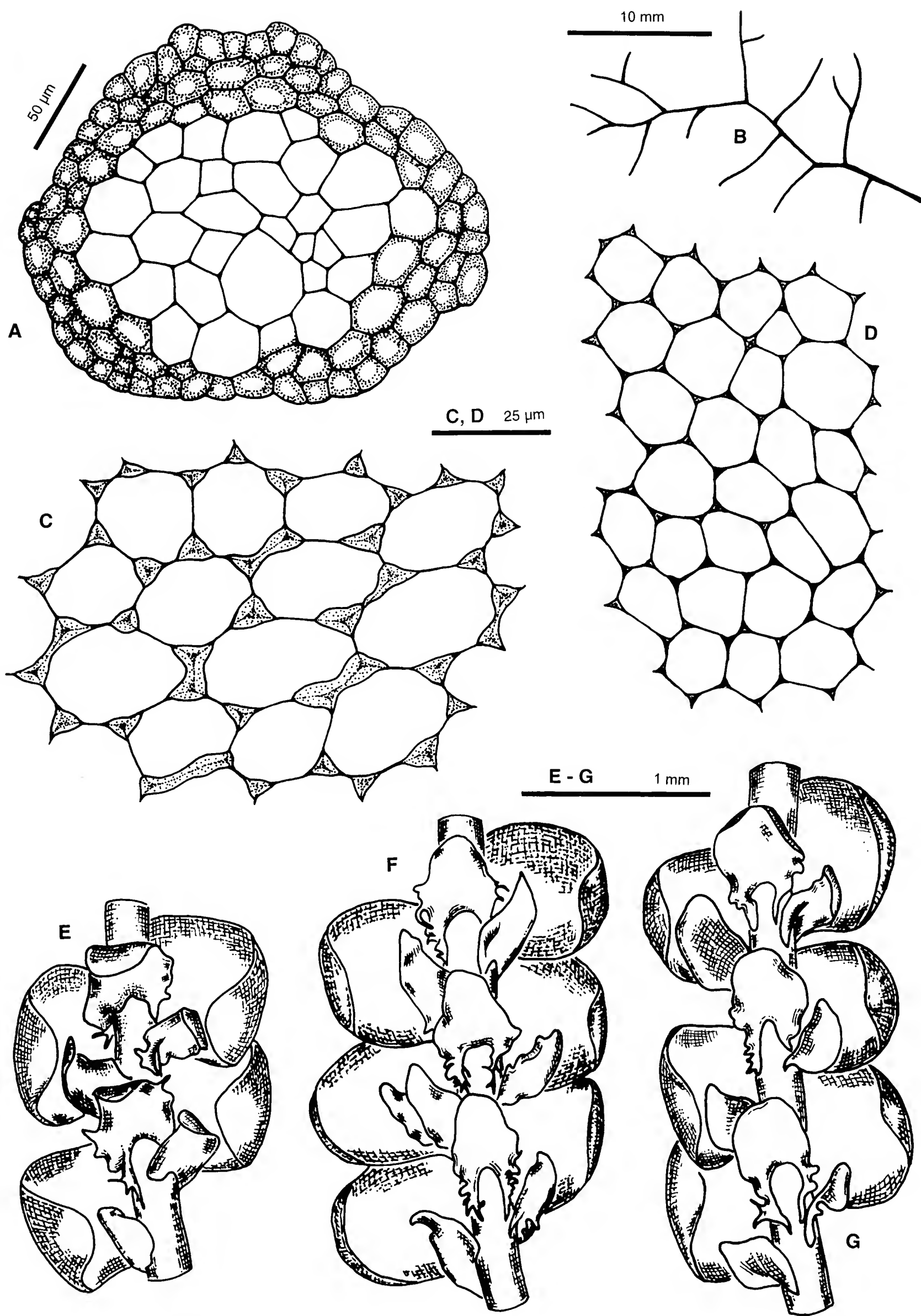


FIG. 1. *Porella gracillima* Mitt. subsp. *urogea* (C. Massal.) S. Hatt. & M. X. Zhang: (A) cross section of stem showing well-developed cortex; (B) habit; (C) basal leaf lobe cells; (D) cells from upper third of leaf lobe; (E, F) parts of shoots, ventral view; (F) one lobe has double lobule. [(A-E, G) from *Davison 6713*, Tennessee (GOET); (F) from *Davison 6720*, Tennessee (UNAF)]

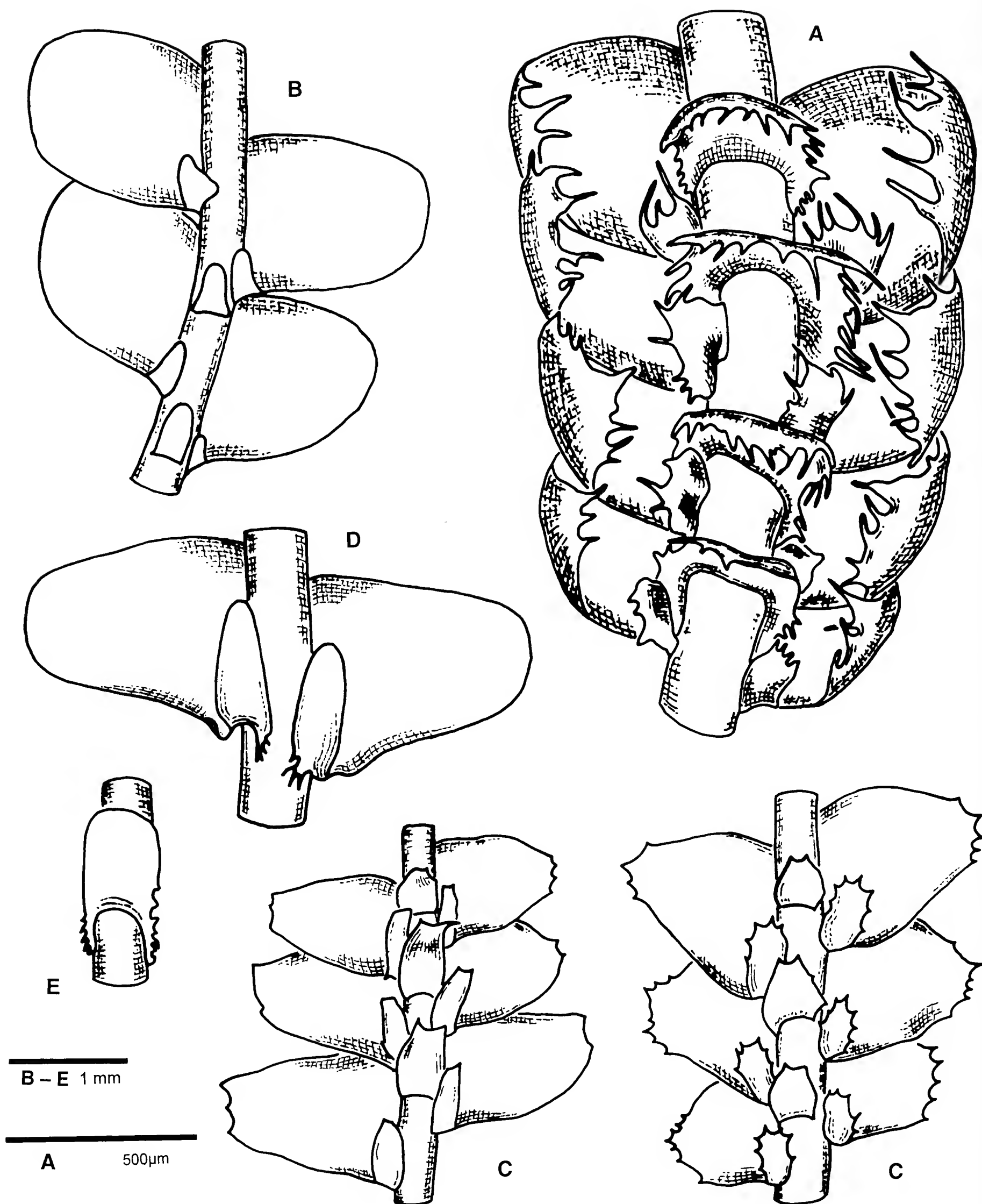


FIG. 2. *Porella fauriei* (Steph.) S. Hatt. (A); *P. pinnata* L. (B); *P. japonica* (Sande Lac.) Mitt. (C); *P. swartziana* (F. Weber) Trevis. (D, E). (A–D) parts of shoots, ventral view; (E) stem fragment with underleaf. [(A) from Tanaka 7339, Japan (HIRO); (B) from Brant 2991, Missouri, USA (GOET); (C) from Deguchi 36624, Japan (HIRO); (D, E) from Churchill et al. 23302, Bolivia (GOET)]

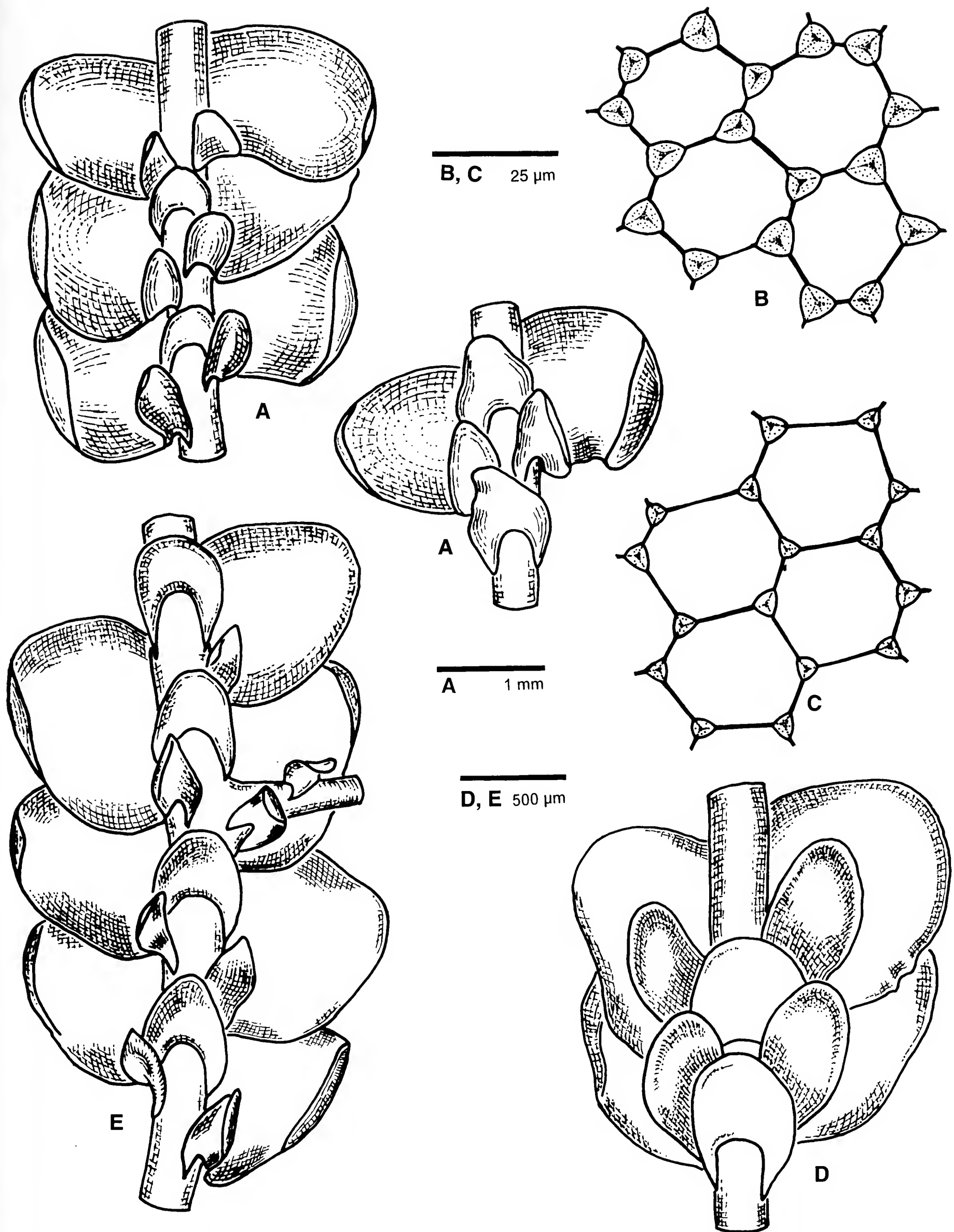


FIG. 3. *Porella navicularis* (Lehm. & Lindenb.) Pfeiff. (A, B); *P. platyphylla* (L.) Pfeiff. (C, D); *P. cordaeana* (Huebener) Moore (E). (A, D, E) parts of shoots, ventral view; (B, C) cells from upper leaf half. [(A, B) from Doyle 11387, California, USA (GOET); (C, D) from Schofield 106589, Canada (UBC); (E) from Schofield 117519, Alaska, USA (UBC)]

Huebener, *Brachythecium* sp., *Campylium chrysophyllum* (Brid.) Lange, *Porella platyphylla* (L.) Pfeiff., *Radula quadrata* Gottsche, and *Thamnobryum alleghaniense* (Müll. Hal.) Nieuwl. On the basis of intermittent visits to the area through May 2007, the populations have been stable since the initial discovery.

Biogeography of *P. gracillima*

The discovery of this Asian element in the Appalachian Mountains adds to numerous Appalachian–East Asiatic disjunctions of bryophytes (e.g., *Porella japonica*, *Diplophyllum andrewsii* A. Evans, *Schwetschkeopsis fabronia* (Schwägr.) Broth., *Fissidens hyalinus* Hook. & Wilson, and vascular plants; e.g. Gray, 1846; Florin, 1963). Iwatsuki (1958) states that as many as 53% of the mosses of the southern Appalachian Mountains are also a common element of the Japanese moss flora. Wide parts of the Appalachians and East Asia escaped pleistocenic glaciations. Sharp (1972) and Schuster (1983) therefore assumed that the Appalachian–East Asiatic disjunctions could be the result of rather recent extinction processes related to the pleistocenic climate changes. The extensive sequence similarities of the Asian and North American *P. gracillima* accessions in the molecular study of

Hentschel et al. (2007) would indeed support rather recent extinction events that led to the fragmentation of a once continuous area, or a recent dispersal scenario, most likely from Asia to North America.

Key to *Porella* in North America

The following key is based on Frye and Clark (1946), Müller (1951–1958), Hattori (1971), Schuster (1980), Hong (1983), Piippo and Norris (1996), Paton (1999), Damsholt (2002), So (2005), and our own observations of North American and European material. With the use of the key, all leaf characters of stem leaves from the central part of vigorous vegetative shoots should be examined. The potassium iodide color reaction is a valuable tool for identifying *Porella* species (Piippo & Norris, 1996) and was used to test all North American species accepted in this study. North American and European specimens of *P. platyphylla* show a distinct potassium iodide color reaction (Piippo & Norris, 1996; our observations). In contrast, Hattori (1976) emphasized that almost all *P. platyphylla* specimens from northern Asia and the Caucasus region that he examined did not show a conspicuous color reaction. To allow for the identification of both *P. platyphylla* types, the species is coded twice.

- 1 Leaf lobes dentate 2
- 1* Lobes entire or with a few blunt teeth 3
- 2 Lobes strongly involute (Fig. 2) *P. fauriei*
- 2* Lobes not or only weakly involute (Fig. 2) *P. japonica*
- 3 Plants turn dark violet to blackish with potassium iodide color reaction 4
- 3* No potassium iodide color reaction 6
- 4 Lobules at inner base with few long cilia; margins of underleaf bases ciliate-dentate (Fig. 2) *P. swartziana*
- 4* Lobules and underleaves without cilia; if lobules or underleaves decurrent, the decurrent strips sinuate-lobed to sinuate-dentate, rarely with a few cilia 5
- 5 Lobules distinctly decurrent below level of keel; underleaves distant; perianth mouth sinuate-crenulate (Fig. 3) *P. cordaeana*
- 5* Lobules not or slightly decurrent below level of keel; underleaves generally imbricate or approximate; perianth mouth dentate-ciliate (Fig. 3) *P. platyphylla*
- 6 Lobules and underleaves small, not or scarcely wider than stem; lobules not decurrent (Fig. 2) *P. pinnata*
- 6* Lobules and/or underleaves larger, at least underleaves wider than stem; lobules short to long decurrent 7
- 7 Lobes strongly involute; shoots slender, up to 1.5 mm wide (Fig. 1)..... *P. gracillima*
- 7* Lobes not or weakly involute; shoots rather robust, more than 1.5 mm wide 8

- 8 Plants sparsely branched, 1–(2)-pinnate; lobules long decurrent; median leaf cells with small triangular thickenings; female branches without normal leaves (Fig. 4) *P. bolanderi*
- 8* Plants abundantly branched, usually bipinnate; lobules short decurrent; if moderately decurrent, median leaf cells with nodulose thickenings; female branches with at least a few small normal leaves 9
- 9 Underleaves up to twice as wide as adjacent lobules; underleaf bases sometimes dentate (Fig. 4) *P. roellii*
- 9* Underleaves more or less as wide as adjacent lobules; underleaf bases usually entire 10
- 10 Plants glossy; trigones large, nodulose; lobules short to moderately decurrent (Fig. 3) *P. navicularis*
- 10* Plants dull; trigones distinct but scarcely bulging, triangular; lobules not or hardly decurrent (Fig. 3)..... *P. platyphylla*

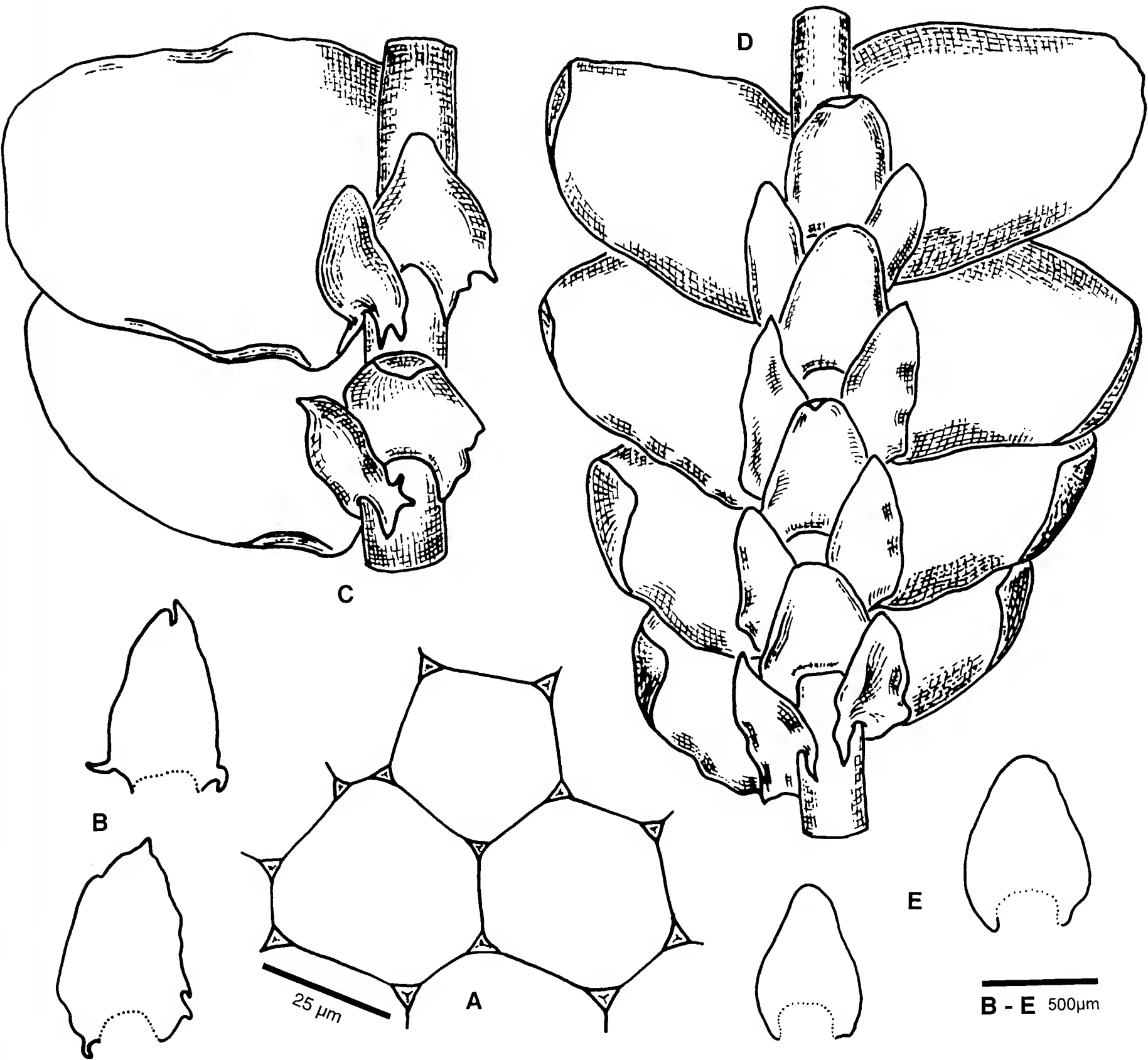


FIG. 4. *Porella bolanderi* (Austin) Pearson (A–C) and *P. roellii* Steph. (D, E). (A) Cells from upper leaf half; (B, E) underleaves; (C, D) parts of shoots, ventral view. [(A–C) from *Shevock* 29359, California, USA (GOET); (D) from *Schofield* 112212, Canada (UBC)]

Perspectives

Molecular phylogenetic studies allow for tests of the monophyly of morphological species concepts of liverworts (e.g., Heinrichs et al., 2004; Hentschel et al., 2006; Vanderpoorten & Long, 2006). So far, these studies confirmed previous concepts (e.g., Hartmann et al., 2006) or allowed for a modified interpretation of morphological evidence (e.g., Feldberg & Heinrichs, 2006). A North American accession of *P. gracillima* incorporated in a molecular phylogenetic study formed a monophyletic lineage with *P. gracillima* accessions from Asia (Hentschel et al., 2007), supporting the *P. gracillima* morpho-species concept of Hattori and Zhang (1985). However, inclusion of an accession of the Asian *P. spinulosa* (Steph.) S. Hatt. in this lineage probably pointed at the need for an even broader *P. gracillima* species concept that should be tested on the basis of an extensive sampling from all parts of its range. Hattori (1969, 1970, 1971) distinguished *P. gracillima* from *P. spinulosa* by its more decurrent lobule and lobule shape, as well as by the presence of ciliate-undulate underleaf and lobule appendages, all features that can show extensive infraspecific variation.

Some studies incorporating multiple accessions of a single liverwort taxon showed a correlation with a geographical rather than a morphological pattern (e.g., Hartmann et al., 2006; Vanderpoorten & Long, 2006; Feldberg et al., 2007). It would be a worthwhile undertaking to study the phylogenetic biogeography of disjunct *Porella* species. Such a study would also help clarify the status of *P. pinnata* fo. *wataugensis* and other morphologically circumscribed local taxa.

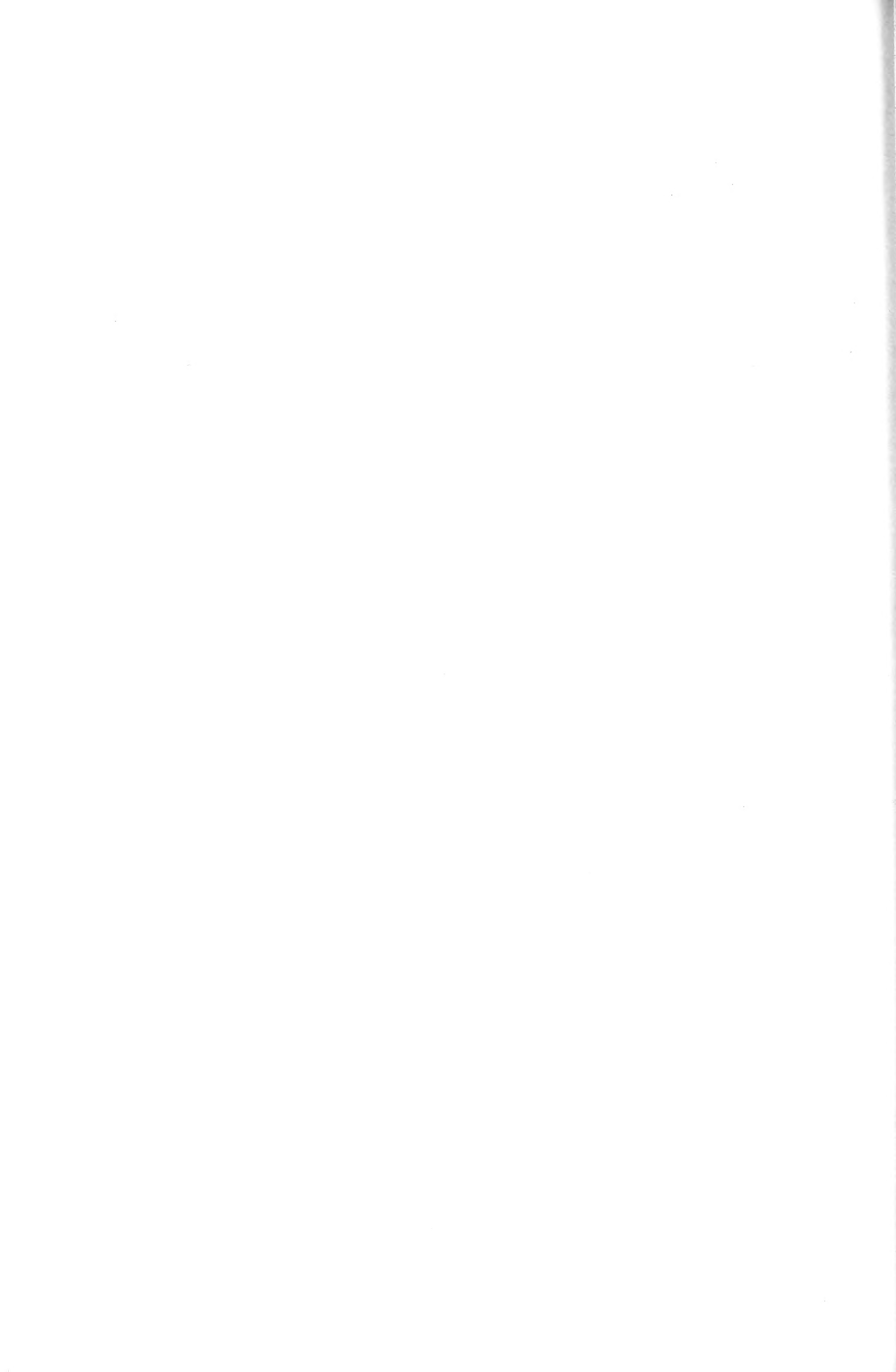
Acknowledgments

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FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Seven: Liverwort Floristics and Revisions— North and South America

Chapter Seventeen: A New Species of *Odontoschisma* (Cephaloziaceae, Marchantiophyta) from South America

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Abstract

The liverwort *Odontoschisma engelii* Gradst. & Burghardt sp. nov. (Cephaloziaceae) is described from páramo vegetation of southern Ecuador and Venezuela. The new species is a member of *Odontoschisma* section *Denudatae* R. M. Schust. and differs from all known species of the genus by the strongly elongated leaves.

Introduction

Odontoschisma (Dumort.) Dumort. (Cephaloziaceae) is a small genus of, at most, 12 species (Gradstein et al., 2001) in the Holarctic and the Tropics. Estimates of ca. 30 species (e.g., Damsholt, 2002) are erroneous and ignore the excessive synonymy in the genus. The genus has a

marked Laurasian distribution, being scarce south of the Equator and unknown from the nontropical regions of the Southern Hemisphere. The southernmost records of the genus are from southern Brazil and Bolivia (Gradstein & Costa, 2003; Gradstein et al., 2003), South Africa (Wigginton & Grolle, 1996), and New Caledonia (So, 2004). The largest diversity of *Odontoschisma*

is in the New World, where about eight species occur, including six in North America (*O. elongatum* (Lindb.) Evans, *O. gibbsiae* A. Evans, *O. macounii* (Austin) Underw., *O. prostratum* (Sw.) Trevis., *O. denudatum* (Mart.) Dumort., *O. sphagni* (Dicks.) Dumort.) and five in Central and South America (*O. brasiliense* Steph., *O. denudatum* (Mart.) Dumort., *O. falcifolium* Steph., *O. longiflorum* (Taylor) Trevis., *O. prostratum* (Sw.) Trevis.; further Neotropical species recognized by Fulford [1968] are synonyms or taxonomically doubtful).

Odontoschisma is a morphologically well-defined genus, being characterized by unlobed leaves that tend to be laterally attached to the stem; rigid stems with undifferentiated epidermis; large, finely segmented oil bodies; reduced underleaves; ventral stolons; gametoecea usually on short ventral branches; dioicous sexuality, and frequent presence of leaf-borne gemmae. Schuster (1974) divided the genus into three sections, on the basis mainly of the presence or absence of a leaf border, gemmae, and branching type: 1) sect. *Odontoschisma* (leaf border present, gemmae lacking, branching exclusively ventral; ca. 5 species); 2) sect. *Denudatae* R. M. Schust. (leaf border absent, gemmae present, branching lateral and ventral; 5–6 species); and 3) sect. *Macounii* R. M. Schust. (like *Denudatae* but lacking secondary pigmentation; *O. macounii* only). The naturalness of this subdivision needs testing by a molecular phylogenetic approach.

Species definitions in the genus remain poorly understood, especially among the tropical taxa, and are in need of revision. In view of the plasticity of the species characters, in particular cell wall thickening, cuticle papillosity, and plant color (Gradstein, 1996; Paton, 1999), a taxonomic revision would require examination of a large series of specimens from all parts of the geographical range of the genus and careful observation of the morphological variation of the species in the field. Also, a study of the genetic structure and molecular differentiation of the species, which has not yet been undertaken, might help improve our understanding of the taxonomy of the genus.

In the course of fieldwork in the Andes of southern Ecuador, the first author collected an apparently undescribed species of *Odontoschisma*. The new species is clearly different from all the known species of the genus by the strongly elongated leaves. We dedicate this new species to Dr. John Engel in honor of his important contributions to hepaticology.

Taxonomic Treatment

Odontoschisma engelii Gradst. & Burghardt, sp. nov. Figures 1, 2

SYNONYM—*Odontoschisma alpinum* R. M. Schust., Nova Hedwigia 119: 83. 2002, nom. inval. (without Latin description). Material: Venezuela, Estado Mérida, Sierra Nevada de Mérida, La Aguáda, lower margin of páramo, 3350 m, R. M. Schuster 76-1623 (hb. Schuster?); the material has not been available for study.

LATIN DESCRIPTION—Ab aliis *Odontoschisma* speciebus foliis anguste elongatis differt.

TYPE—**Ecuador. Loja:** Cordillera Oriental, Parque Nacional Podocarpus, Cajanuma, lower margin of páramo, 3150 m, on the vertical, slightly overhanging and partially shaded side of a large, crystalline boulder in the páramo, at the junction of the trail leading to the lakes and the “mirador,” forming dense, low, brownish mats, 19 September 2006, S. R. Gradstein, S. Léon-Yáñez & J. Santiana 10178 (holotype, GOET, c. gyn. and gemmae; isotype, QCA).

DESCRIPTION—Plants prostrate to ascending, in dense, low, green to reddish-brown mats. Stems to 10 mm long with leafy shoots to 0.8 mm wide, becoming microphyllous and gemmiferous distally, irregularly branched, the branches lateral-intercalary (leafy shoots) or ventral-intercalary (leafless stolons), stolons frequently present, terminal branching lacking. Stems ca. 150 mm in diameter, in cross section ca. 8–10 cells high, composed of thick-walled cells, the epidermis cells similar to inner cells or slightly smaller. Leaves succubous, on microphyllous branches subtransverse, imbricate, concave, suberect to spreading, narrowly elongate and somewhat asymmetrically falcate, ca. 2× as long as wide, ca. 0.5 mm long and 250–270 µm wide, margins somewhat tapering to a narrowly rounded tip, insertion line extending to dorsal midline of stem, not leaving a leaf-free strip. Leaf cells subisodiametric, in midleaf 25–30 × 25 µm, the walls with large, irregularly bulging trigones, cell lumina angular; leaf surfaces smooth; oil bodies present in all cells, colorless, *Jungermannia*-type, large, 2–5 per cell, rounded to ellipsoid, finely papillose-segmented. Underleaves vestigial, ovate-elongate or subulate, ca. 3–5 cells long, undivided, without slime papillae. Rhizoids colorless, scarce, scattered, present only on stolons and bases of gynoecial shoots. Gemmae produced on the upper portions of ascending microphyllous shoots,



FIG. 1. *Odontoschisma engelii*. **Top**, overview of the habitat of *O. engelii*; the new species grows in the upper left corner of the overhanging rock face; persons from left to right: N. Cumbicus, S. R. Gradstein (observing mat of *O. engelii*), J. Santiana (seen at back), S. León-Yáñez. **Bottom**, mat of *O. engelii*. (Photographs by H. Behling)

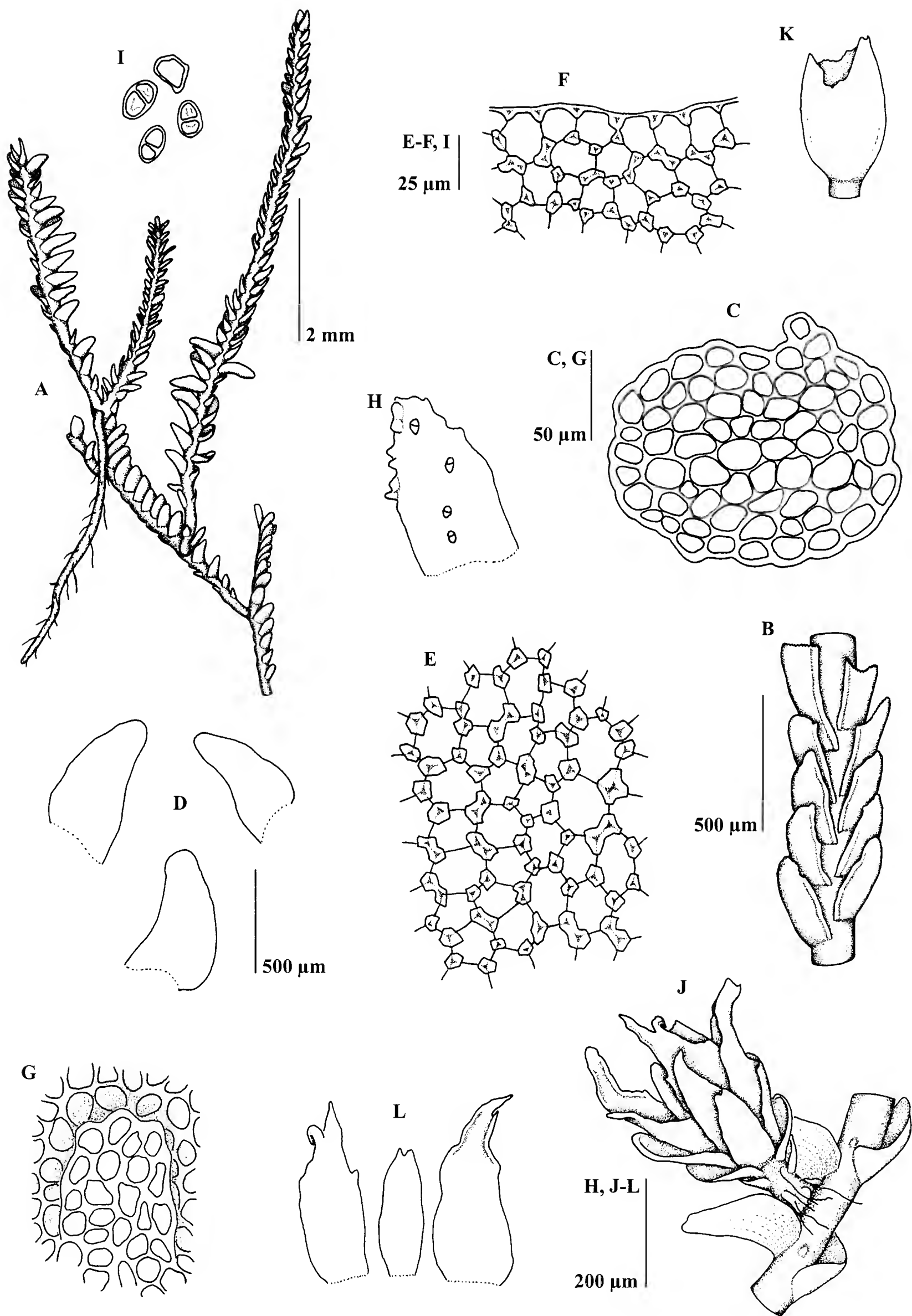


FIG. 2. *Odontoschisma engelii*. (A) Habit in ventral view; (B) portion of shoot in dorsal view, showing leaf insertions; (C) stem cross section; (D) leaves; (E) midleaf cells; (F) leaf margin cells; (G) underleaf; (H) gemmiferous leaf; (I) gemmae; (J) gynoeclial branch; (K) immature perianth; (L) inner female bract and bracteole. All drawn from the paratype.

arising from leaf margins, colorless to wine-reddish, ellipsoid to slightly angular, (1–)2-celled, 18–20 μm long, and 12–15 μm wide, slightly thick-walled, smooth; margins of gemmiferous leaves typically erose.

Dioicous (?); androecia not seen. Gynoecia colorless, on very short ventral or ventrolateral branches and often associated with a stolon; bracts and bracteoles in two series, the bracts about as long as leaves; inner bracts shallowly and unevenly bifid (to 0.2), the dorsal lobe longer than the ventral one, apices obtuse to acute, margins entire or crenulate by prominent wall thickenings; inner bracteole free from the bracts, narrowly elongate, slightly shorter than bracts, shallowly bifid, apices obtuse. Perianth (immature) fusiform, with a wide, undulate, \pm entire (?; only partial remains available) mouth. Sporophyte lacking.

DISTRIBUTION AND HABITAT—Venezuela (3350 m), Ecuador (3150 m), in moist, lower páramo vegetation, known from two locations only. In the type locality (Ecuador), the species occurs on the overhanging face of a large, steep, crystalline boulder (Fig. 1), together with *Adelanthus decipiens* (Hook.) Mitt., *Anastrophyllum stellatum* R. M. Schust. (= *A. gradsteinii* Váña), *Isotachis lopezii* (R. M. Schust.) Gradst., and *Kurzia capillaris* (Sw.) Grolle. The substrate at the Venezuelan locality is unknown.

ADDITIONAL SPECIMEN EXAMINED—Type locality, 8 August 2003, S. R. Gradstein & N. Mandl 10151 (paratypes, GOET, QCA).

Discussion

Odontoschisma engelii is a member of the section *Denudatae* by the presence of lateral and ventral branching, by the presence of gemmae, the absence of a leaf border, and by the reddish-brown plant color. The new species is clearly separated from other members of sect. *Denudatae* and from all other species of the genus as a whole, by its narrowly elongate, ca. 2 \times as long as wide leaves. In other species of *Odontoschisma* the leaves are rounded, ovate, or short rectangular, ca. 1.0–1.5 \times longer than wide. The new species was earlier recorded by Schuster (2002) from Venezuelan páramo as *O. alpinum* R. M. Schust. The latter name was proposed without description, however, and is invalid.

Odontoschisma denudatum is the only other member of the genus recorded from Neotropical páramo (Gradstein [1999]; *O. atropurpureum* Steph. recorded from Neotropical páramo is a synonym of *O. denudatum* according to Gradstein & Costa [2003]). The new species is separated from *O. denudatum*, however, by the elongated leaves and the smooth leaf surfaces. Further notable features of *O. engelii* include the insertion of the leaves, which extends clearly to the dorsal midline of the stem (usually not extending to the dorsal midline in most other members of the genus), the lack of slime papillae on underleaves, the wine-red gemmae, and the long microphyllous branches with densely imbricate, subtransverse leaves. Branching in the new species is ventral-intercalary (stolons and most of the gynoecial branches) or lateral-intercalary (leafy shoots; some gynoecial branches). The lateral branches in *O. engelii* invariably originate from the ventral side of the lateral merophytes.

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FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Seven: Liverwort Floristics and Revisions— North and South America

Chapter Eighteen: A Revision of *Tylimanthus* (Acrobolbaceae, Marchantiophyta) in Tropical America, Africa, and Macaronesia

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Abstract

Taxonomic revision of the liverwort genus *Tylimanthus* Mitt. (Acrobolbaceae) in tropical America, Africa, and Macaronesia leads to the recognition of one widespread and variable species, *T. laxus* (Lehm. & Lindenb.) Spruce. *Tylimanthus approximatus* (Lindenb.) Besch., *T. azoricus* Grolle & Perss., *T. fendleri* (Gottsche) Steph., *T. herzogii* Steph., *T. madeirensis* Grolle & Perss., *T. ruwenzorensis* S. W. Arnell, *T. setaceo-ciliatus* Steph., *T. striolatus* Steph., and *T. subtilis* Steph. are new synonyms of *T. laxus*, and *T. bispinosus* J. B. Jack & Steph. and *T. cuneifolius* Steph. are excluded from *Tylimanthus*. Lectotypes are proposed for *T. approximatus*, *T. herzogii*, and *T. laxus*.

Introduction

Tylimanthus Mitt. is a rather small genus of leafy liverworts with about 100 published

binomials (Geissler & Bischler, 1990) and 20–30 currently accepted species (Gradstein et al., 2001). The genus is mainly Southern Hemispheric in distribution, extending northward to Central

America and tropical Africa, as well as to Macaronesia, and is characteristic of humid temperate and tropical-montane habitats. *Tylimanthus* is a member of Acrobolbaceae subfam. Acrobolboideae, together with the genera *Acrobolbus* Nees and *Marsupidium* Mitt. (Schuster, 2001), and is distinguished by the pendent marsupium positioned terminal on the main axis, intercalary branching, papillose cuticle of stem and leaves, narrow ventral merophyte (not wider than 5 cell rows), vestigial underleaves and dioicous condition. Species of *Tylimanthus* can be confusingly similar to members of the genus *Plagiochila* (Dumort.) Dumort. but differ from the latter by the marsupium, which is lacking in *Plagiochila*.

Mitten (1867) established the genus *Tylimanthus* on the basis of *Jungermannia saccata* Hook., replacing in part the older name *Gymnanthe* Taylor ex. Lehm. (nom. illeg.). This was a considerable improvement because the latter genus was very heterogeneous and contained species now placed in five different genera (*Acrobolbus*, *Balantiopsis* Mitt., *Gongylanthus* Nees, *Notoscyphus* Mitt., *Tylimanthus*). The genus *Tylimanthus* has generally been accepted since, although its separation from *Acrobolbus* and *Marsupidium* has been questioned. Although Grolle (1963) and Engel and Grolle (1971) kept the three genera apart, Hässel de Menéndez and Solari (1972) united *Tylimanthus* and *Marsupidium* into one broad genus *Tylimanthus*. Recent authors usually accept the three as separate genera (Schuster, 1980; Scott, 1985; Grolle, 1989a; Glenney, 1998; Gradstein et al., 2001), although with some doubt (e.g., Schuster, 2001). Stech et al. (2006) in a molecular-phylogenetic analysis of Acrobolbaceae could not separate *Acrobolbus*, *Marsupidium*, and *Tylimanthus* at the generic level. However, because only one accession each of *Acrobolbus* and *Marsupidium* was sequenced, the results were preliminary and required further study.

The first tropical species of *Tylimanthus* were described from Guadeloupe by Lehmann and Lindenberg (Lindenberg, 1840), as *Plagiochila approximata* Lindenb. and *P. laxa* Lehm. & Lindenb. *Plagiochila laxa* was subsequently transferred to *Tylimanthus* by Spruce (1884–1885) and *P. approximata* by Bescherelle (1893). The most comprehensive treatment of *Tylimanthus* to date is by Stephani (1905–1908, 1917–1924) in *Species hepaticarum*, who recognized 56 species, including 43 (!) new ones. Many of these have in the meantime been reduced to synonymy, but those

of tropical America (17 species) have not yet been revised. Stephani also made a first attempt to subdivide the genus by proposing two informal groups, “*Integrifolii*,” including species with edentate leaves, and “*Dentifolii*,” with dentate leaves; the latter group was further subdivided on the basis of leaf shape. This classification was clearly artificial, however, and was generally ignored by later authors.

A first formal infrageneric classification of *Tylimanthus* was proposed by Grolle (in Grolle & Persson, 1966), who recognized two sections: sect. *Anisodon* Grolle, with rhizoids on leaf margins, and sect. *Tylimanthus*, without rhizoids on leaf margins. Species of tropical America, Africa, and Macaronesia, together with *T. integrifolius* A. Evans from Hawaii, belong to sect. *Anisodon*, and the remaining to sect. *Tylimanthus*.

In this paper, we present a taxonomic revision of the genus *Tylimanthus* from tropical America, Africa, and Macaronesia. The results show the occurrence in this region of one widespread and variable species, *T. laxus* (Lehm. & Lindenb.) Spruce. Detailed description and illustration of *T. laxus* are presented below.

Taxonomic Treatment

Tylimanthus laxus (Lehm. & Lindenb.) Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 502. 1885; *Plagiochila laxa* Lehm. & Lindenb. in Lindenberg, Sp. Hepat.: 68. 1840; *Gymnanthe laxa* (Lehm. & Lindenb.) Gottsche, Ann. Sci. Nat. Paris 5, 1: 137. 1864. Type. Guadeloupe, ex hb. Hooker (lectotype, here designated, w [male]; isolectotypes, s-B80312 [male], s-B80336, s-B80337 [male], s-B80338, s-B80339 [male]). Figs. 1–4.

Plagiochila approximata Lindenb., Sp. Hep.: 59. 1840; *Tylimanthus approximatus* (Lindenb.) Besch., J. Bot. (Morot) 7: 191. 1893. Type. Guadeloupe, ex hb. Hooker (lectotype, here designated, w [female], “mis. Hooker 1837 N. 28”; isolectotypes, s-B39393 [female], s-B39394 [female]), *syn. nov.*

The date of valid publication of the basionym of *Tylimanthus approximatus* is the same as that of *T. laxus*. Both appeared in the same fascicle of the *Species Hepaticarum* of Lindenberg. The name *T. laxus* is chosen here as the preferred name of the species because it has been used more often (e.g., Spruce, 1884–1885; Jones, 1980; Gradstein & Costa, 2003; Stech et al., 2006).

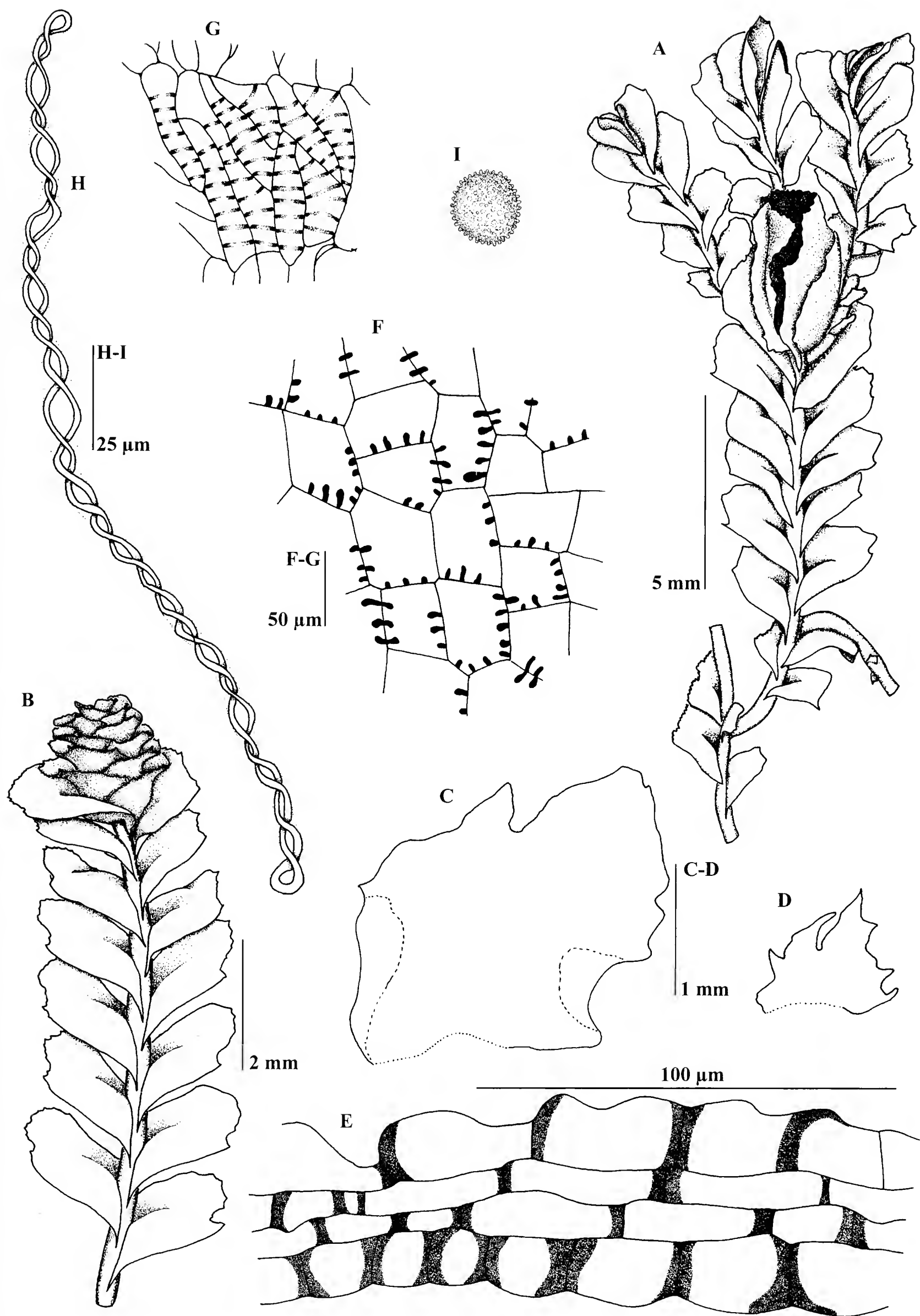


FIG. 1. *Tylimanthus laxus*. (A) Part of female plant with unfertilized archegonia, dorsal view; (B) part of male plant with terminal androecia, dorsal view; (C) outer female bract; (D) innermost female bract; (E) cross section of capsule wall; (F) outer capsule wall cells; (G) inner capsule wall cells; (H) elater; (I) spore. [(A) from *Gradstein 10147* (GOET); (B) from *Heinrichs et al. 4486* (GOET); (C, D) from *Gradstein 9690* (GOET); (E-I) from *Gradstein 9648* (GOET)]

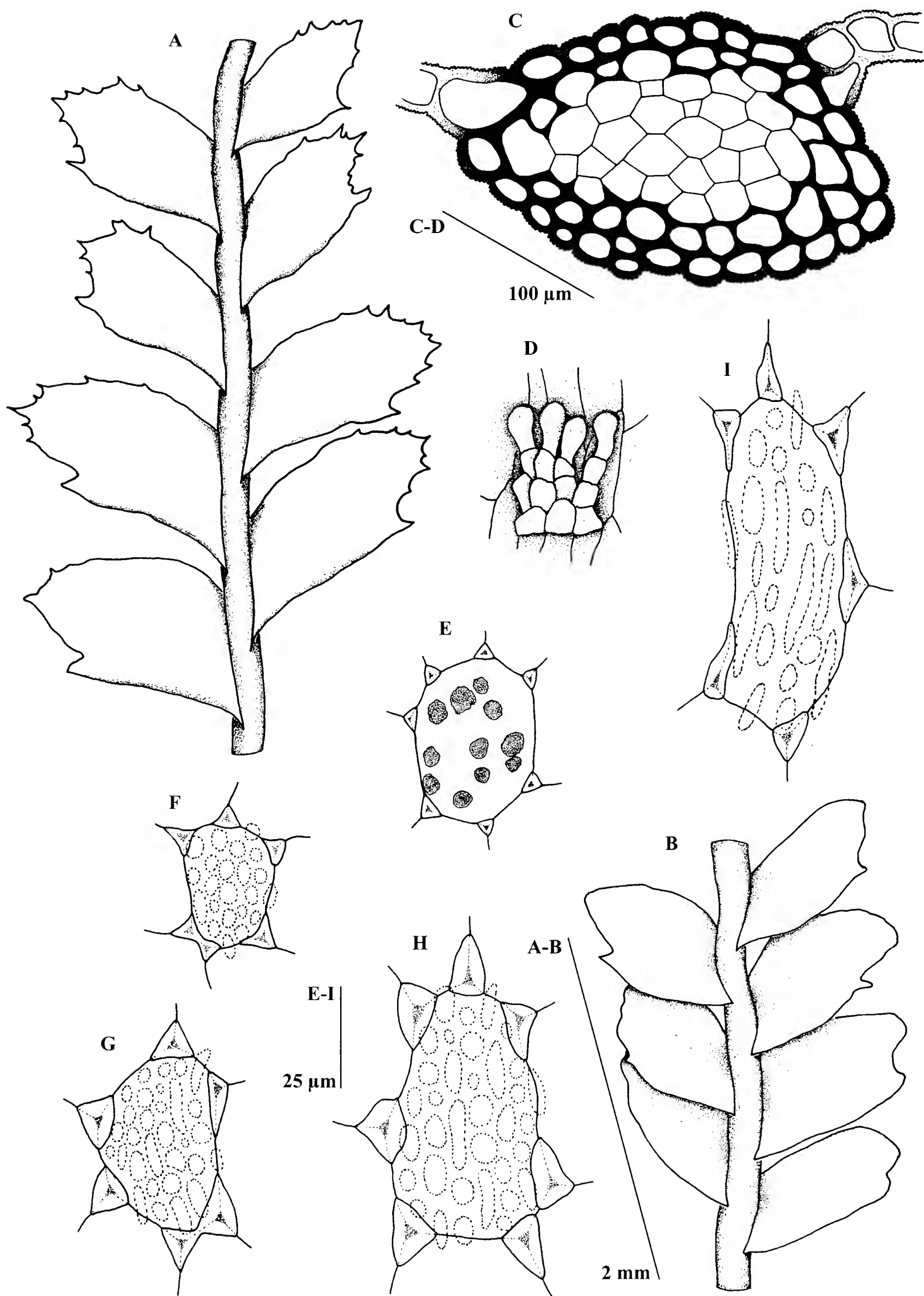


FIG. 2. *Tylimanthus laxus*. (A, B) Part of shoot, dorsal view; (C) cross section of stem; (D) underleaf; (E) median leaf cell with oil bodies (papillae not drawn); (F–H) median leaf cells; (I) basal leaf cell. [(A, D) from the holotype of *T. subtilis* (G-9521); (B, F) from *Een & Persson s.n.* (JE-H3157); (C) from *Hegewald 7994* (MO-5223130); (E) from *Heinrichs et al. 4486* (GOET); (G) from *Cleef 1289* (GOET); (H, I) from the holotype of *T. setaceo-ciliatus* (G-9517)]

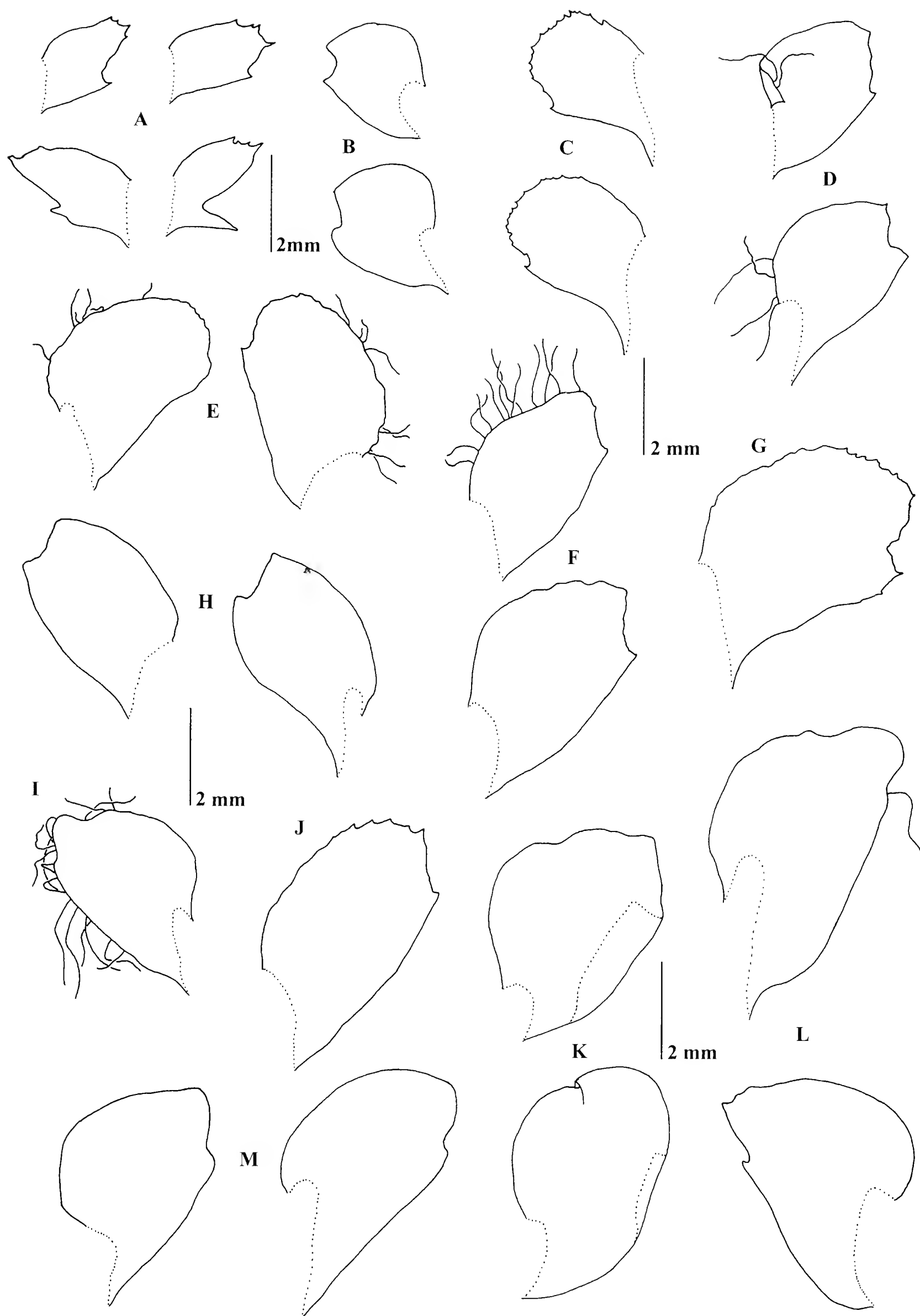


FIG. 3. *Tylimanthus laxus*. (A–M) Leaves, showing variation in shape. [(A) From the holotype of *T. subtilis* (G-9521); (B) from Cleef 6502a (U); (C) from Heinrichs et al. 4486 (GOET); (D) from Cleef 1289 (U); (E) from Hegewald 7994 (MO-5223130); (F) from Frahm et al. 1252 (GOET); (G) from Gradstein et al. 6744 (U); (H) from Gradstein 4238 (U); (I) from the holotype of *T. setaceo-ciliatus* (G-9517); (J) from the isotype of *Gymnanthe fendleri* (w-2296); (K) from Aguirre & Gradstein 1298 (U); (L) from Preußing et al. 03103 (STU); (M) from Gradstein et al. 3453 (U)]

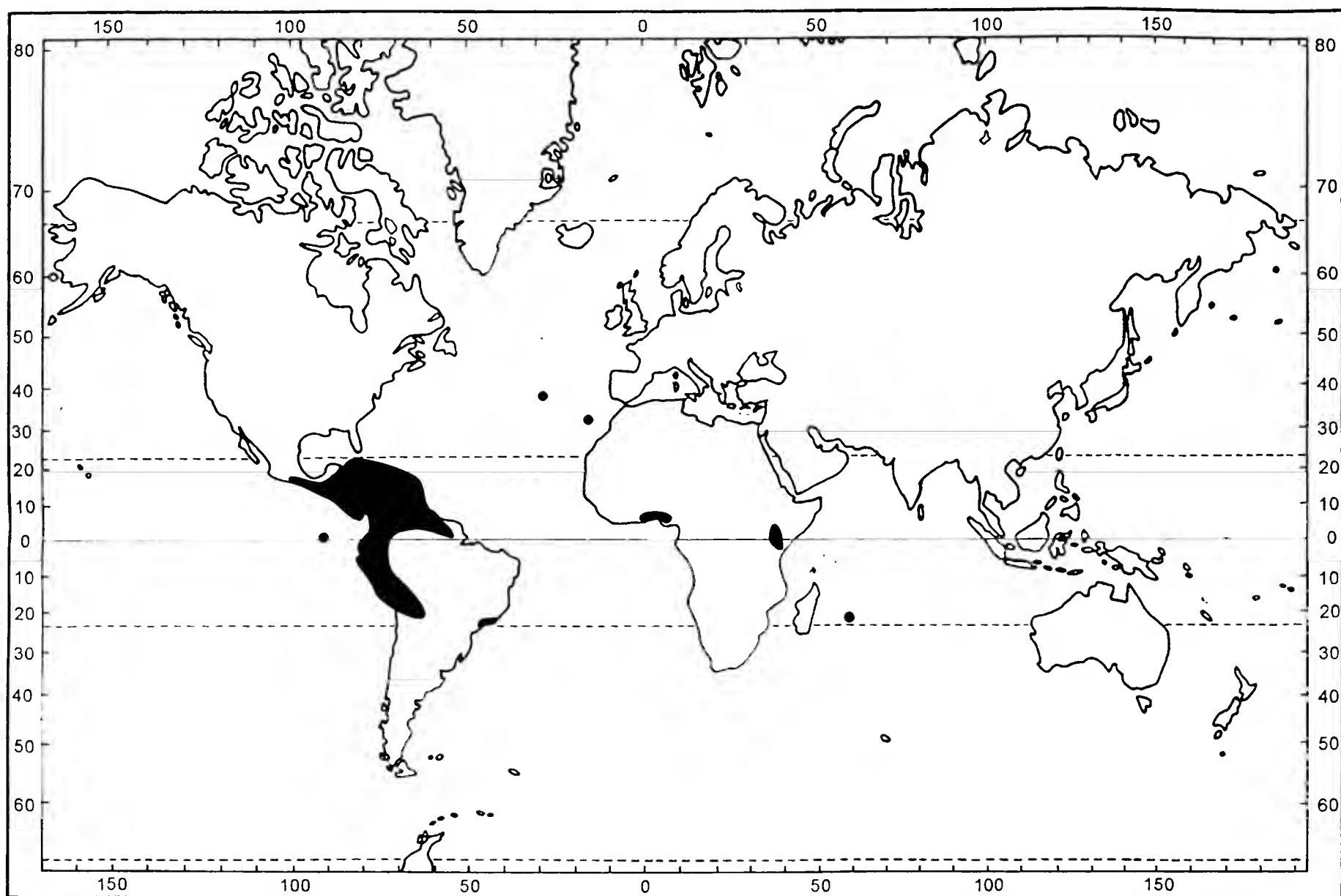


FIG. 4. Distribution of *Tylimanthus laxus*.

Gymnanthe fendleri Gottsche, Ann. Sci. Nat. Paris 5, 1: 136. 1864; *Tylimanthus fendleri* (Gottsche) Steph., Spec. Hepat. 3: 11. 1905, nom. illeg. (Art. 53.1). Type. Venezuela, Valencia, *Fendler s.n.* (holotype, B, presumably destroyed [not seen]; isotypes, G-024301 [female], w-2296 [female]), *syn. nov.*

Tylimanthus striolatus Steph., Spec. Hepat. 3: 4. 1905. Type. Bolivia. "Cochabamba, prope Choquecamata," 1889, *W. Germain s.n.* (holotype, G-24129), *syn. nov.*

Tylimanthus subtilis Steph., Spec. Hepat. 6: 252. 1922. Type. Suriname. "Guiana batava, Suringar legit," 1886 (holotype, G-9521), *syn. nov.*

Tylimanthus jamaicensis Steph., Spec. Hepat. 3: 9. 1905. Type. Jamaica. *Eggers 3767a* (holotype, G-9448 [female]), *syn. fide Fulford* (1987).

Tylimanthus herzogii Steph. in Herzog, Biblioth. Bot. 87, 2: 215. 1916. Type. Bolivia. "Im Nebelwald über Comarapa, 2600 m," *Herzog 4280* (lectotype, here designated, JE [female]; isolectotypes, s-B48576 [female], w [female]), *syn. nov.*

Although Stephani (1916) cites two collections (*Herzog 4258, 4280*) with the original description,

none of them was available among the materials examined from G. Therefore, an original specimen from the Herzog herbarium in JE is selected as the lectotype.

Tylimanthus setaceo-ciliatus Steph., Spec. Hepat. 6: 252. 1922. Type. Ecuador. "ad pedras in paramo del Matanga, sat frequens via ad guodaquiza," V. Bomboiza, *Allioni s.n.* (holotype, G-9517 [male] as *T. setaceus*; isotype, JE-H3598), *syn. nov.*

Tylimanthus ruwenzorensis S. W. Arnell, Ark. Bot. (ser. 2) 3: 560. 1957. Type. Uganda, Mobuke valley, *Hedberg 339lf* (holotype, UPS, not seen; isotype, s-B48587), *syn. nov.*

Tylimanthus aetiopicus S. W. Arnell, Svensk Bot. Tidskr. 54: 192. 1960. Type. Ethiopia, Garamba, *Eriksson s.n.* (holotype, s-B80308 [female]; isotype, JE [female], s-B80307).

Tylimanthus azoricus Grolle & Perss., Svensk Bot. Tidskr. 60: 169. 1966. Type. Portugal, Azores, Flores, Lagoa Rasa near Lagens, 400 m, 24.8.1937, *Allorge s.n.* (holotype, s-48106; isotypes, JE-H3155), *syn. nov.*

Tylimanthus madeirensis Grolle & Perss., Svensk Bot. Tidskr. 60: 166. 1966. Type. Portugal, Madeira, Fanal, Seixal region of North

Madeira, *de Nobrega s.n.* (holotype, s; isotype, JE-H3159), *syn. nov.*

?*Marsupidium latifolium* R. M. Schust., *Phytologia* 39: 249. 1978. Type. Venezuela, Estado Tachira, Paramo de Tama, 3100 m *Schuster & Ruiz-Teran 76-1940c* (holotype, herb. Schuster, not seen).

ILLUSTRATIONS—Arnell (1956, fig. 23 as *Tylimanthus ruwenzorensis*; 1960, fig. 3 as *T. aethiopicus*); Grolle & Persson (1966, fig. 2 as *T. madeirensis*, fig. 3 as *T. azoricus*); Jones (1980, fig. a as *T. ruwenzorensis*); Lindenberg (1840, fig. VIII as *P. approximata*; fig. XVIII as *P. laxa*); Schuster (1980, fig. 610 as *Tylimanthus* sp.); Stephani (1916, fig. 152 as *T. herzogii*; 1985, figs. 10340, 10341 as *T. approximatus*, fig. 10349 as *T. herzogii*, fig. 10354 as *T. laxus*, fig. 10364 as *T. setaceo-ciliatus*, fig. 10372 as *T. jamaicensis*, fig. 10376 as *T. striolatus*, fig. 10377 as *T. subtilis*, fig. 10396 as *T. fendleri*); Wiggington (2004, fig. 123 as *T. ruwenzorensis*).

Plants 1.5–15 cm long, 2–5(–6) mm wide, pale whitish green to yellowish green, turning brownish in the herbarium, growing in diffuse to dense patches with creeping stoloniferous microphyllous shoots giving rise to upright, scarcely branched secondary leafy stems. Branching sparse, exclusively intercalary and usually lateral, occasionally ventral. Rhizoids arising in fascicles from ventral leaf bases and singly from leaf margins, lower parts of stems and stolons. Stems light to dark brown, (150–)230–320(–360) × (100–)150–250(–275) µm in diameter, mostly dorsoventrally compressed with more or less differentiated cortex and medulla, epidermis cells in surface view 2–3 times as long as wide, outer surface of epidermis cells slightly to strongly papillose; stem in cross section about (8–)10–16 cells wide and (7–)10–14 cells high, with a brownish cortex consisting of 1–2 layers of regularly thick-walled cells, cortical cells 16–25(–30) × 10–17(–26) µm, medullary cells colorless, thin-walled, without wall thickenings or rarely with small triangular thickenings in the outer rows, larger in size than cortical cells, (25–)28–35(–50) × (15–)23–27(–45) µm. Leaves succubous, alternate, remote to densely imbricate, broad ovate to obovate-lingulate to lingulate, (0.8–)1.4–2.0(–2.5) × (0.6–)1.0–1.4(–1.6) mm, (1–)1.2–2(–2.5) times as long as wide; leaf apex obliquely truncate, often asymmetrically bilobed to 0.3(–0.9) to weakly emarginate, leaf margins entire to irregularly dentate with 8–15(–20) small, triangular teeth consisting of 2 basal and 1 apical cell (rarely coarse with 3–4 basal cells and 3–5

apical cells), frequently with marginal rhizoids, rarely with an indistinct border of 1 row of pellucid cells, leaf insertion-line J-shaped, dorsal margin strongly convex-recurved to plane, the leaf otherwise plane, ventral leaf bases not too moderately expanded, reaching ± across the stem, not or very short decurrent up to 0.1 leaf length, dorsal leaf bases not decurrent or, occasionally, long decurrent up to 0.3(–0.5) leaf length. Leaf areolation ± regular, cells in midleaf (28–)33–43(–53) × (14–)23–30(–35) µm, 1.1–1.6(–2) times as long as wide, basal leaf cells (45–)54–65(–70) × (19–)20–30(–33) µm, 1.5–3.5 times as long as wide; trigones small triangular to nodulose, rarely trabeculate, not elongated on long cell walls; oil bodies in median leaf cells 8–18 per cell, globose to broadly ellipsoidal, 5–7 µm long, pale yellowish hyaline to brownish, finely papillose; leaf cuticle papillose, in upper half of leaf with 20–40(–60) predominantly rounded papillae, each papilla 2–5 µm in diameter, in lower half with 15–30 predominantly fusiform papillae, 3–7 times as long as wide, 18–25 × 4–6 µm (Fig. 2G–H). Underleaves very small or lacking, present in the youngest parts of the plant, 3–5 cells wide and 2–3 cells high, often terminated by slime papillae. Vegetative reproduction by leaf fragmentation.

Dioicous, female plants usually more vigorous than male ones. Androecia in short to long terminal spikes on leading shoots, occasionally becoming intercalary; bracts in (4–)5–10(–19) pairs, closely imbricate, in transition zone to leaves less strongly imbricate or remote, with somewhat elongated, leaf-like distal part, basal part of bracts strongly inflated, distal part obliquely to horizontally spreading, opposite bracts overlapping to 0.3 of the width of the saccate basal part, areolation similar to vegetative leaves, but trigones of the inflated basal part much weaker; (1–)2–5 antheridia per bract, antheridial stalk composed of 2 cell rows.

Gynoecia always terminal on upright, elongated, leafy stems, often unfertilized, then frequently innovated from below or within the bracts; outer bracts distinctly larger than vegetative leaves, generally more deeply incised and with coarser dentition, to 3 mm long and 3 mm wide, ovate to broadly ovate to nearly circinate, margins occasionally undulate, with up to 13–20, 1–5-cell-long teeth; areolation similar to that of vegetative leaves but trigones larger; innermost bract much smaller than outer bracts, singly, ca. 1–1.2 mm long and 1–1.1 mm wide, asymmetrically bilobed

to 0.5 and coarsely toothed; bracteoles lacking; archegonia numerous, unfertilized ones remaining on top of the marsupium. Marsupium at sporophyte maturity short-cylindrical, 4–4.5 mm long and 1.5–1.7 mm wide, ca. 3 times as long as wide, pendent, densely rhizoid-covered, not penetrating into the substrate. Perianth lacking. Seta substantially exserted. Capsule cylindrical with an acute tip, capsule valves 2–2.5 mm long and 0.5–0.8 mm wide, capsule wall 43–55 μm thick, of 4–5 cell layers, thickenings present in radial and tangential walls of all cell layers, epidermal cells in surface view subquadrate to short rectangular, 30–59 \times 31–55 μm , with 3–5 nodulose, brown thickenings on most longitudinal walls and 3–4 thickenings on most transverse walls, innermost cells in surface view elongate, 61–148 \times 17–37 μm , 1.8–6.7 times as long as wide, transversely to somewhat irregularly arranged, with ladder-like thickenings. Spores 19–26 μm in diameter, globose, 1-cellular, spore surface with densely spaced bacula. Elaters bispiral, linear, 5–7 μm wide.

DISTRIBUTION (FIG. 4)—*Tylimanthus laxus* is widespread in tropical America, from southern Mexico southward to Bolivia and southeastern Brazil. Additionally, the species occurs in the Azores and Madeira, where it was previously known as *T. azoricus* and *T. madeirensis*, respectively, and in Africa (Ghana, Nigeria, Uganda, Tanzania, La Réunion), where it was known as *T. ruwenzorensis*. *Tylimanthus laxus* occurs in natural and disturbed humid evergreen forests at elevations from 100 to 4000 m and is most common between 1200 and 3000 m on the mainland and at lower elevations (500–1000 m) on islands. The species inhabits a wide range of substrates, including soil, humus, damp rock, tree trunks, twigs, and branches and has frequently been recorded from rocks in the vicinity of cataracts.

SELECTED SPECIMENS EXAMINED—MEXICO. **CHIAPAS:** Cinco Lagunas, Lagos de Montebello National Park, 1600 m, *Breedlove* 67907 (MO-3683932). **HONDURAS.** **LEMPIRA:** Montaña de Celaque, Rio Arcagual SW of Gracias, 2480 m, *Allen* 11500 (MO-3982137). **NICARAGUA.** **GRANADA:** Volcán Mombacho, 1000–1222 m, *Henrich & Moreno* 192 (GOET, U). **COSTA RICA.** **ALAJUELA:** Volcán Poás, 2600–2700 m, *Gradstein & Mues* 9628 (GOET). **HEREDIA:** Volcán Barva, 2650–2900 m, *Gradstein & Mues* 9648 (GOET). **PUNTARENAS:** Reserva Biológica Monteverde, 1550 m, *Gradstein* 9487, 9595, 9605 (GOET). **SAN JOSÉ:** Cerro de la Muerte, 3250 m, *Holz* CR 00-0197 (GOET, MO-5282873, s-B62214); *ibid.*, Reserva 3 de

Junio, 2650–2800 m, *Gradstein & Mues* 9686, 9690 (GOET); *ibid.*, Los Nubes, 1500–1800 m, *Standley* 38740 (s-B80331). **PANAMA.** **DARIÉN:** Cerro Pirre, 800–1150 m, *Salazar-Allen & Gradstein s.n.* (JE-H3600). **CUBA.** **ORIENTE:** Sierra Maestra, “La Bayamesa,” 1925 m, *Ekman* 7177a (s-B80334); *ibid.*, Punta de Palma Mocho, 1350 m, *Ekman* 5237b (s-B80332); *ibid.*, Pico Turquino, 2040 m, *Ekman* 14568 (JE, s-B80333). **JAMAICA.** Abbey Grees, *Underwood* 2530-a (JE); Morce’s Gap, 1175–1500 m, *Maxon & Killip* 1294 (JE, s-B80313); Whitfield Hall, 1600–1700 m, *Hegewald* 7994 (MO-5223130). **PUERTO RICO.** Mt. El Toro, 1075 m, *Gradstein* 6556 (GOET, U). **DOMINICA.** Mt. Diablotin, *Elliot* 658 (JE); between Pont Cassé and Emerald Pool, 500 m, *Schäfer-Verwimp & Verwimp* 17717 (GOET). **GUADELOUPE.** Basse Terre, trail to first “Chute des Carbets,” 700–900 m, *Gradstein & Sastre de Jesus* 6619, 6623, 6626 (GOET, U); Forêt des Bains Jaunes, *Allorge s.n.* (G-9451, MO-2568333, s-B80310, U); La Découverte, 600–950 m, *Husnot s.n.* (G-9462, G-10206/15, JE, s-B80309, s-B80311). **MARTINIQUE.** Morne Paillasse, *Duss* 424 (JE). **TRINIDAD.** s.l. *Crüger* 130 (G-9401). **COLOMBIA.** **BOYACÁ:** N of Belén, Cerro Pan d’Azucar, 4000 m, *Cleef* 9822 (GOET, JE, MO-2565946, s-B80294, U). **CASANARE:** La Salina, El Arenal, 2650 m, *Aguirre et al.* 3206 (GOET, U). **CUNDINAMARCA:** Páramo de Chingaza, trail to St. Juanito, 3400 m, *Gradstein* 4237, 4238 (GOET, U); Páramo between Cogua and San Cayetano, Laguna Verde, 3670–3675 m, *Cleef* 6323, 6501, 6502a (GOET, U); Páramo de Palacio, Cobeceras Río Negro, 3370 m, *Cleef* 5140 (GOET, U). **META:** Cerro Nevado del Sumapaz, 3615 m, *Cleef* 1286, 1289 (GOET, U). **NARIÑO:** road Pasto—Laguna de la Cocha, 3100 m, *Churchill & Arbelaez* 15943 (GOET, U). **RISARALDA:** trail to Puerto de Oro, W of Mistrato, 1600 m, *Gradstein* 8501 (GOET); Santa Rosa, Finca La Sierra, 3710 m, *Aguirre & Gradstein* 1298 (GOET, U). **TOLIMA:** Nevado de Tolima, 3750 m, v.d. *Hammen & Jaramillo* 3232 (JE); Santa Isabel, Finca El Ochoral, 3000 m, *Aguirre & Gradstein* 1529 (GOET, U). **VENEZUELA.** **MÉRIDA:** Sierra de St. Domingo, Páramo de Mucuchies, 3500 m, *Oberwinkler & Poelt* HV69-150 (JE). **GUYANA.** **UPPER MAZARUNI DISTRICT:** North slope of Mt. Roraima, 1200–1600 m, *Gradstein* 5295, 5305, 5414, 5442 (GOET, JE, U). **ECUADOR.** **CARCHI:** road Tulcán—Maldonado, Páramo El Angel, 3900 m, *Gradstein* 6849 (GOET, JE, U); road Tulcán—El Angel, on crest of divide, 3630 m, *Gradstein et al.* 3453 (GOET, U). **GALAPAGOS ISLANDS:** Isabela, Vulcán Alcedo, 1100 m, v. d. *Werff* 1267a (JE); Isabela, Vulcán Cerro Azul, 700–800 m, *Gradstein & Sipman* H 419 (GOET, U); Santiago, 800 m, *Pike* B-41366 (JE). **LOJA:** Cajanuma, 2800–3100 m, *Gradstein & Mandl* 10147 (GOET).

PICHINCHA: road Quito—Mindo km 62, 2350 m, *Heinrichs et al.* 4486 (GOET); old road Quito—St. Domingo, 3000 m, *Gradstein et al.* 6744 (GOET, JE, U). **ZAMORA CHINCHIPE:** Parque National Podocarpus, Bombuscaro W of Zamora, 1050 m, *Schäfer-Verwimp & Preußing* MPE 03069 (STU), *ibid.*, 2400 m, *Preußing et al.* MPE 03039, 2300 m, 03103 (STU); Reserva Biológica San Francisco ca. 30 km E of Loja, 2100 m, *Joßberger & Preußing* MPE 03018, 03033, 03034 (STU); Pass El Tiro, road Loja—Zamora, 2650–2700 m, *Preußing et al.* MPE 03102, 03065, 03101 (STU). **BRAZIL.** **ESPIRITO SANTO:** Serra de Caparaó, 2020 m, *Schäfer-Verwimp & Verwimp* 11540 (JE). **RIO DE JANEIRO:** Serro do Itatiaia, Campo Belo, 2400 m, *Costa & Gradstein* 3809 (GOET); Itatiaia, near entrance of Parque Nac. Itatiaia, 500 m, *Costa & Gradstein* 3898 (GOET). **SAO PAULO:** Ilha de Sao Sebastio, 100 m, *Schäfer-Verwimp & Verwimp* 12450 (JE); Ubatuba, 750 m, *Schäfer-Verwimp & Verwimp* 7643 (GOET, JE, MO-5271356); Serra do Mar between Bertiooga and Mogi das Cruzes, 450 m, *Schäfer-Verwimp & Verwimp* 9009 (MO-5271357). **PERU.** **CUZCO:** Saxarhuamán, *Herrera* 3120/2 (S-B80295). **RIOJA:** San Martin, road Chachapoyas—Moyobamba, 1900 m, *Frahm et al.* 1252 (U, JE). **BOLIVIA.** **LA PAZ:** road La Paz—Coroico, 3000–3200 m, *Gradstein* 7054 (GOET, U). **PORTUGAL.** **AZORES:** Flores, Ribeira Grande, 600 m, *Allorge s.n.* (S-B80328); Pico, Furmas de Pico, 1500 m *Persson s.n.* (S-B80329); Pico, Serra Grande, 800 m, *V. & P. Allorge s.n.* (S-B80327); Pico, San Miguel, Lagoa do Fogo, *Schwab* SN 123 (JE). **MADEIRA:** Montado Chão near Ribeiro Frio, 1000 m, *Een & Persson s.n.* (JE-H3158); Encumeada da Vincente, Pico Torrinhas, 1000–1200 m, *Een & Persson s.n.* (JE-H3157). **UGANDA.** **RUWENZORI:** Bujuku Valley near Lake Bujuku, 4000 m, *Hedberg* 703g (S-B80306); *Hedberg s.n.* (JE). **TANZANIA.** Morogoro District: Uluguru Mts., Mgeta River Valley on E escarpment of Lukwangule Plateau, 2250–2350 m, *Pócs et al.* 88113/G (G); *ibid.*, ridge E of Magari Peak, 2000–2100 m, *Pócs et al.* 6297/R (G-910058, GOET, U). **RÉUNION.** S slopes of Piton de la Fournaise, 650–800 m, *Pócs* 9503/Y (G-427404); Pas de Bellecombe, *Barclay* 2136 (JE); trail Piton des Neiges, 1500 m, *Grimalac* 70.R.4540 (JE); Hautes de Saint Denis, 1200 m, *Onraedt* 71.R.9249/b (JE), *ibid.*, 1400–1800 m, *Een* R275 (S-B13029).

Discussion

Tylimanthus laxus as circumscribed here is a highly variable species, especially in habit and

leaf characters (Figs. 1–3). We have been unable to find clear-cut morphological discontinuities among the types and additional specimens investigated, allowing us to recognize more than one taxon. Leaf arrangement varies from distant to imbricate, leaf shape from lingulate to almost rounded (*T. setaceo-ciliatus*), leaf apex from truncate to bilobed, and leaf margins from irregularly toothed to entire. Plants from lower montane forests of the Lesser Antilles, including the lectotype of *T. laxus*, are often quite slender with remote foliation and rather narrowly elongate leaves. These plants probably refer to pendent epiphytic forms. The type of *T. approximatus*, on the other hand, is representative of phenotypes with imbricate foliation and rather broad leaves with a more or less truncate leaf apex (Figs. 1B, 3C,E). Stephani (1905–1908) separated the latter species from *T. laxus* by the lack of papillosity (see also Gradstein & Costa, 2003); however, our study of the type and other specimens assigned to *T. approximatus* revealed the presence of a papillose cuticle in the latter, even though papillae are rather low. The type of *T. subtilis* (Figs. 2A,D, 3A) is unusual in having undivided to deeply asymmetrically bifid leaves (divided to more than half of leaf length), weak stems only 7–8 cells in diameter and without distinct cortex, and large leaf cells measuring to 60 µm in length and 35 µm in width in midleaf; this seems to be a phenotype of deeply shaded habitats. *Tylimanthus herzogii* is a robust, female phenotype of *T. laxus* with rather coarsely toothed leaves and nodulose trigones, and *T. striolatus* is a poor, sterile form with edentate lingulate leaves.

Tylimanthus setaceo-ciliatus is a high-elevation form of *T. laxus* with rather broad, ovate to almost rounded leaves with entire margins (but frequent occurrence of marginal rhizoids, Fig. 3I) and yellowish-green plant color, never pale to whitish green as often observed in *T. laxus*. This phenotype is characteristic of páramo and open forest near the timberline and occurs in the high Andes as well as in eastern Africa (Ruwenzori, *Hedberg* 703g). Interestingly, capsules in these high-elevation plants have walls 4 cell layers thick, with cells of the inner layer mostly less than 100 µm long (Fig. 1E,G). In plants from lower elevations, on the other hand, walls are normally 5-layered and inner cells over 100 µm long. Because we were able to study only a limited number of sporophytic populations, we refrain to attain taxonomic importance to these differences.

Marsupidium latifolium R. M. Schust., described from Venezuelan páramo and only known from the type, is tentatively treated as a synonymy of *T. laxus*. We have not been able to study the type, but judging from the original description, this plant represents the high-elevation form of *T. laxus* described as *T. setaceo-ciliatus*.

Plants from Macaronesia described as *T. azoricus* and *T. madeirensis*, and from Africa as *T. ruwenzorensis* and its synonyms, all fit in the variation observed in Neotropical populations of *T. laxus*. The conspecificity of *T. ruwenzorensis* and *T. laxus* was already suggested by Jones (1980) and Stech et al. (2006). The rather small leaf cell size considered diagnostic of *T. madeirensis* is not uncommon in *T. laxus*.

Tylimanthus laxus as circumscribed here is distinguished from other species of the genus by the presence of rhizoids on leaf margins. By the new definition, the species is equivalent to the section *Anisodon* Grolle, which in addition to the species treated in this paper also included *T. integrifolius* from Hawaii. We have not studied the latter species but would expect it to belong to *T. laxus* as well.

Excluded Names

Tylimanthus bifidus Steph. in Herzog, Bibl. Bot. 87: 215. 1916. Type. Bolivia, Nebelwald über Comarapa, *Herzog 3812* (holotype, G).

= *Adelanthus decipiens* (Hook.) Mitt. (fide Grolle, 1972).

Tylimanthus bispinosus J. B. Jack & Steph., Hedwigia 31: 26. 1892; *Acrobolbus bispinosus* (J. B. Jack & Steph.) Steph. Type. Colombia ["Nova Granada"], Ocaña, 1874, *Wallis s.n.* (holotype, G-9411 [male]).

= *Plagiochila* sp.

The material stands out by the smooth cuticle and androecia in long spikes, with male bracts not overlapping dorsally and possessing a rather reduced distal portion unlike in *Tylimanthus*.

Tylimanthus congoensis Steph., Spec. Hepat. 6: 246. 1922. Type. Zaire, *Lerat s.n.* (not seen)

= *Plagiochila integerrima* Steph. (fide Grolle, 1989b).

Tylimanthus cuneifolius Steph., Spec. Hepat. 3:10. 1905. Type. Venezuela, Valencia, *Fendler s.n.* (holotype, G-005730; isotype, S-B5768 [female])

= *Tylimanthus setaceus* Steph., Spec. Hepat. 3:10. 1905. Type. Colombia ["Nova Granada"], Dept. Antioquia, Páramo de Sonson, 1872, *Wallis s.n.* (holotype, G-24128)

= *Acrobolbus* sp.

This species belong in *Acrobolbus* because of the prostrate, not upright nor ascending habit, lack of basal stolons, and stems lacking differentiation into cortex and medulla. Moreover, the almost symmetrically bilobed leaves with pointed lobes of *T. cuneifolius* are typical of *Acrobolbus* and are not observed in *Tylimanthus*. Similar specimens have been observed from Ecuador (e.g., Cordillera de Llanganates, near Las Torres, *Asplund s.n.*, S-B80293).

Tylimanthus madagascariensis Steph., Rev. Bryol. 28: 95. 1901, nom. inval., Art. 32.1/c). Type. Madagascar, Tamatave, *Perrot 1195* (holotype, G).

= *Kymatocalyx madagascariensis* (Steph.) Gradst. & Vána (fide Grolle, 1963; Gradstein & Vána, 1999).

Tylimanthus marginatus Steph. Spec. Hepat. 3: 5. 1905. Type. Martinique, 780 m, *Duss 22* (lectotype, G).

= *Plagiochila bicornis* Hampe & Gottsche. (fide H. Inoue in Grolle, 1991).

Tylimanthus pittierii Steph. Spec. Hepat. 6: 250. 1922. Type. Costa Rica, *Pittier & Durand 6058* (holotype, G).

= *Adelanthus pittieri* (Steph.) Grolle (fide Grolle, 1972).

Tylimanthus pusillus Steph. in Herzog, Bibl. Bot. 87: 216. 1916. Type. Bolivia, Viloco, 4600 m, 1911, *Herzog 3117* (holotype, G-9486; isotypes, JE, M).

= *Adelanthus decipiens* (Hook.) Mitt. (fide Grolle, 1989b).

Tylimanthus retusus Steph. Spec. Hepat. 6: 251. 1922. Type. Cameroon, *Mildbraed s.n.* (not seen).

= *Plagiochila integerrima* Steph. (fide Grolle, 1989b).

Tylimanthus schweinfurthii Steph., Spec. Hepat. 3: 8. 1905. Type. Central Africa, *Schweinfurth s.n.* (not seen).

= *Plagiochila integerrima* Steph. (fide Grolle, 1989b).

Tylimanthus typhacellus Gottsche ex Herzog, Rev. Bryol. Lichénol. 23: 38. 1954., nom. inval. Art. 32.1(c); *Clasmatocolea typhacella* Steph., Icones Ineditae 10366, nom. inval. Original material. Brazil, *Puiggari 847* (G, not seen; M).

= *Myriocoleopsis fluviatilis* (Steph.) Reiner & Gradst. (fide Grolle, 1957; Reiner-Drehwald & Gradstein, 1997).

Tylimanthus wilmsii Steph., Spec. Hepat. 6: 252. 1922. Type. South Africa, Cape Town, *Wilms s.n.* (not seen).

= *Marsupidium limbatum* (Steph.) Grolle (fide Grolle, 1965).

Unrevised Names

Tylimanthus africanus Pears., Kristiania Vidensk.-Selsk. Forhandl. 1887 (9): 14. 1887. Type. South Africa, Knysna, 1883, *H. Iversen s.n.* (not seen).

Jones (1980) considered this species a possible form of *T. ruwenzorensis*, but Grolle (1995) suggested a close relationship to *T. tenellus* (Hook. f. & Taylor) Mitt.

Tylimanthus anisodontus (Hook. f. & Taylor) Mitt., in Meliss, St. Helena: 368. 1875. [as *T. anisodon*]. Type. St. Helena, *Hooker s.n.* (not seen).

This species stands out by acutely pointed leaf lobes with elongated terminal cells (Grolle & Persson, 1966). We have not studied the type specimen, but judging from the description, this species might fit into the variation of *T. laxus*.

T. strictolomus Spruce ex Besch., J. Bot (Morot) 7: 191. 1893, nom. inval., Art. 32.1(c). Original material. Guadeloupe, *L'Herminier* 57, 58 (not seen).

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Dedication

This paper is contributed in honor of our respected colleague John J. Engel on the occasion of his 40 years of scientific publications and his distinguished career at the Field Museum.

Abstract

The bryophyte flora of the Pacific Northwest includes three previously known species of tuber-producing hornworts that occupy seasonally dry habitats. Except for *Phymatoceros bulbiculosus* (Brot.) Stotler, W.T. Doyle & Crand.-Stotl., which was recently segregated

from *Phaeoceros* Prosk. on the basis of a combination of morphological and molecular studies, no comprehensive studies of these taxa have been undertaken since their naming. As a consequence, confusion exists regarding their taxonomic identity. This study combines field observations with morphological and molecular data to evaluate the systematic status of *Phaeoceros hallii* (Austin) Prosk. and *Phaeoceros pearsonii* (M. Howe) Prosk. These data support the recognition of a new species, *Phaeoceros proskaueri* Stotler, Crand.-Stotl. & W. T. Doyle, in this complex of related taxa. In addition, morphological studies of the lectotype of *Anthoceros tuberosus* Taylor (= *Phaeoceros tuberosus* (Taylor) Prosk.), which is formally designated here, and the holotype of *Paraphymatoceros diadematus* Hässel demonstrate that neither is related to *P. hallii*, *P. pearsonii* or *P. proskaueri*. *Phaeoceros tuberosus* is aligned with *P. laevis* (L.) Prosk. and *Paraphymatoceros hallii* (Austin) Hässel is placed as a synonym of *Phaeoceros hallii*. *Paraphymatoceros diadematus* is postulated to be congeneric with *Phaeomegaceros* Duff et al., and the following new combinations are made: *Paraphymatoceros fimbriatus* (Gottsche) Stotler, *Paraphymatoceros coriaceus* (Steph.) Stotler, *Paraphymatoceros hirticalyx* (Steph.) Stotler, and *Paraphymatoceros skottsbergii* (Steph.) Stotler.

Introduction

The foothills and valleys of the coastal and central mountains of Washington, Oregon, and California support several species of hornworts that perennate through the long dry summers by forming tubers at the conclusion of their abbreviated winter to early spring reproductive growth cycles (Doyle & Stotler, 2006). Included among these are *Phaeoceros hallii* (Austin) Prosk. and *P. pearsonii* (M. Howe) Prosk., both characterized by somewhat flattened, apical, and/or marginal tubers and *Phymatoceros bulbiculosus* (Brot.) Stotler, W. T. Doyle & Crand.-Stotl. [including *Anthoceros phymatodes* M. Howe (Crandall-Stotler et al., 2006)], which bears stalked ventral tubers. Recent studies have confirmed that the latter taxon is not only morphologically distinct from other tuber-producing species of *Phaeoceros* Prosk. (Crandall-Stotler et al., 2006) but, in fact, comprises a separate lineage in hornwort phylogeny (Duff et al., 2007). *Phaeoceros hallii* and *P. pearsonii*, which occupy similar habitats as *Phymatoceros* Stotler, W. T. Doyle & Crand.-Stotl., are resolved as sister taxa in a lineage that is weakly supported as part of the *Phaeoceros* clade (Duff et al., 2007: fig. 4). Although recognized as distinct taxa in systematic treatments since Howe (1898), diagnostic descriptions of these two species have typically focused on features of mature sporophytes and spores (e.g., Hässel de Menéndez, 1989; Hasegawa, 1991), leaving many details of their gametophyte morphologies unrecorded. As intimated by Proskauer (1957) and Schuster (1992), an overreliance on

spore morphology confounds species identification, especially since spore wall architecture can change during late stages of maturation (Crandall-Stotler et al., 2006). Our studies of gametophytes as well as sporophytes in numerous herbarium collections of anthocerototes from California, coupled with extensive field monitoring of populations, have convinced us that there is in the *P. hallii* – *P. pearsonii* complex a previously undescribed tuber-bearing element that shares features with each of these species but is nonetheless distinct from both. This study was undertaken to clarify the systematic circumscriptions of *P. hallii* and *P. pearsonii* and evaluate the taxonomic status of this element, employing a total evidence approach.

Taxonomic History

Austin (1875) recognized 14 species in his treatment on the hornworts of North America, nine of which were newly described. Five of the new species, namely *Anthoceros fusiformis* Austin, *A. hallii* Austin, *A. oregonus* Austin, *A. stomatifer* Austin, and *A. sulcatus* Austin, were based completely or in part on collections made by Elihu Hall in Oregon. With each of the specimen packets, Austin wrote “R. Mt. Hall” or what perhaps was “R. Mts. Hall.” We observed this notation with the types of *A. hallii*, *A. oregonus*, and *A. sulcatus*, and Howe (1898) recorded it for *A. fusiformis* and *A. stomatifer*. Regardless, Austin never made mention of this in any of his

publications, and we presume that it was simply an identifier, since Hall was a well-known Rocky Mountain naturalist. Ewan (1950) pointed out that Hall collected plants in the Rocky Mountains of central Colorado in 1862 and that his specimens were poorly labeled, with some specimens bearing only the name Hall. It is highly unlikely that Austin would have received any Hall specimens from Colorado because they predated his study of bryophytes, and it is not likely that any of the hornworts that Austin described were from the Rocky Mountains. Although the abbreviation could stand for Round Mountain, located in central Oregon and not far from known Hall collecting sites in Salem and Silverton, Oregon, there is no evidence for that either. Unfortunately, "R. Mt." prompted the annotation "Rocky Mts." to be written on these packets by B. Carrington or W. Pearson, who together purchased the Austin herbarium following his death, and this locality error, Rocky Mountains, has been perpetuated in the literature (e.g., Howe, 1898: 18; Hässel de Menéndez, 1989: 718; Schuster, 1992: 772).

Specimens from three locations were cited by Austin (1875) in his treatment of *Anthoceros hallii*. These included a "fertile plant on the ground" from Silverton, Oregon, and sterile material from dripping rocks, Salem, Oregon, collected by E. Hall. He also reported specimens from "swamps, Marvin [sic = Marin] County, California" collected by H. Bolander with thalli said to be "plicate-costate or lamellate; the lamellae bearing elliptical tubers underneath." In a revision of North American hornworts, Howe (1898) selected the fertile Silverton, Oregon, collection, now in the herbarium of the University of Manchester, Manchester Museum (MANCH), as the lectotype specimen for this name. The sterile material from Salem, Oregon, is likewise in MANCH, but the Bolander specimen is not, nor is it cited in either Howe (1898) or Hässel de Menéndez (1989: 731).

In a discussion of *Anthoceros sulcatus*, Austin (1875) wrote of Hall specimens that he had initially aligned them with the genus *Notothylas* Sull. ex A. Gray and that he had applied the manuscript name of *Notothylas hallii* to them in 1874. That initial generic placement was no doubt prompted at least in part by the rather short capsules that are indehiscent or very imperfectly so. With further study, not only did he reconsider, he concluded "*Notothylas Hallii* MSS" to represent the connecting link between the two genera, prompting his reduction of

Notothylas to *Anthoceros* L. That, of course, necessitated a name change to prevent a later homonym, whereby he chose the epithet "*sulcatus*," in reference to the capsules that were scored with longitudinal furrows. His only specimen citation was "On moist earth, Salem, Oregon, E. Hall." Although Austin (1875) contrasted this species only with *N. orbicularis* (Schwein.) A. Gray, Howe (1898: 11) made mention of studying original specimens with the name "*Notothylas hallii*" (= *A. sulcatus*) and considered them to clearly represent *A. hallii*. Five separate packets of the original material are extant in MANCH.

During his studies of North American hornworts, Howe (1898) described *Anthoceros pearsonii* M. Howe, which he depicted as the commonest yellow-spored taxon of the Pacific coast. It was contrasted with *A. hallii* by the development of capsules that are normally four times longer, by the production of more perfect pseudoelaters, and by distinct spore surface markings. Several populations were recorded, with *Howe 16*, from Mill Valley, Marin County, California, designated as the holotype.

An additional species name that became associated with this complex is *Anthoceros bolanderi* Steph. named by Stephani in 1916. Although Frye and Clark (1947) wrote that they were not able to distinguish *A. bolanderi* from *A. pearsonii*, they did not make a formal reduction. That was done by Hässel de Menéndez (1989: 731), who listed the type "U.S.A. California, Mendocino City, Bolander (ex Herb. Gottsche) (G)" as identical to the entry by Bonner (1962: 171) in *Index Hepaticarum*. Because of a probable printer error, "Hab.," (an abbreviation for place of growth) which routinely followed all of Stephani's entries in the six volumes of *Species Hepaticarum* (Stephani, 1898–1924), is missing after the description of *A. bolanderi*. Unfortunately, there is no certain way to know the collection location other than making the assumption that because it was named in honor of Henry Bolander, that it is likely a Bolander collection, thus likely from California. A collection in the Conservatoire et Jardin Botaniques, Genève (G) with these data in the hand of Stephani represents the original material. Therefore, the specimen referred to in G by Hässel de Menéndez (1989: 731) should be considered the lectotype. A portion of that material also exists at UC.

When Proskauer (1951) segregated the genus *Phaeoceros* from *Anthoceros*, he made a number of new combinations, one being *P. hallii*. At the

same time, he listed *Anthoceros phymatodes* as a synonym of *P. hallii*, on the basis of evidence from cultured plants. It has been recently shown, however, that *A. phymatodes* not only is not related to *P. hallii*, but represents a novel genus described as *Phymatoceros* (Crandall-Stotler et al., 2006). Recently, another interpretation has been proposed regarding *P. hallii*. Hässel de Menéndez (2006) named the hornwort genus *Paraphymatoceros* Hässel on the basis of a new species, *Paraphymatoceros diadematus* Hässel, from Chile. In that same publication she removed *P. hallii* from *Phaeoceros* and transferred it to *Paraphymatoceros*, while retaining *P. pearsonii* in *Phaeoceros*. This once again brings into question the systematic affinities of *P. hallii*. Consequently, although the focus of this study is the delimitation of species within the *P. hallii* complex, we also treat *Paraphymatoceros*.

Materials and Methods

MATERIALS—Morphological features were scored for numerous freshly collected specimens from California and Oregon and a broad sample of herbarium collections, including type specimens of *Anthoceros hallii*, *A. sulcatus*, *A. pearsonii*, *A. tuberosus* Taylor, *A. bolanderi*, and *Paraphymatoceros diadematus*, with a combination of optical and scanning electron microscopy (SEM). A list of specimens examined in addition to those cited in the taxonomic section, is included in the appendix to this manuscript.

MORPHOLOGICAL METHODS—Freshly collected plants from Doyle 11,366 (*P. hallii*) and Doyle 11,328, 11,357, and 11,422 (*Phaeoceros proskaueri* sp. nov.) were fixed in formalin–acetic acid–ethanol (FAA), dehydrated in a graded series of tertiary-butyl alcohol (TBA), and embedded in Paraplast for serial sectioning (Jensen, 1962). Sections were cut at 8 μ m, stained with contrasting Iron Alum Safranin O and 1% Fast Green FCF in 70% ethanol and mounted in Histoclad. Axenic cultures were established from collections of *P. pearsonii* [Doyle 11,377 & Doyle 11,429], *P. hallii* [Doyle 11,366], and *P. proskaueri* sp. nov. [Doyle 11,339], employing the methods of Hatcher (1965) for comparisons with field populations and to provide soil-free material for transmission electron microscopy (TEM) and molecular studies. All phenological data were extracted from field populations sampled over several growing seasons.

Small samples of thalli from the types of *A. tuberosus* and *A. hallii* were restored for SEM following the methods of Hofmann et al. (1996), but with graded replacement of FDA by 100% ethanol before critical point drying (Crandall-Stotler et al., 2006). Freshly collected plants and samples from axenic culture for SEM study were fixed in 2% glutaraldehyde/2% paraformaldehyde in 0.1 M sodium cacodylate at pH 7.2 at 4°C, overnight, postfixed in 2% aqueous OsO₄ for three hours and dehydrated through a graded ethanol series. Both types of samples were critical point dried in a Tousimis Samdri-750 CPD, using CO₂ as the transition fluid, and then mounted on stubs covered with sticky tape. Spore samples were dispersed from air-dried capsules directly onto stubs covered with sticky tape. Samples were coated with 400–450 Å gold-palladium in a Denton Desk II sputter-coater. Specimens were viewed and images captured with either a Hitachi H500 SEM (UC Santa Cruz) or S570 SEM (SIUC).

For TEM, thalli from the axenic culture of *P. proskaueri* sp. nov. (Doyle 11,339) were fixed four hours at 25°C in 2% glutaraldehyde/2% paraformaldehyde in 0.1 M sodium cacodylate buffer, pH 7.2. After three rinses in buffer, they were postfixed in buffered 2% OsO₄, 3.5 hours at 25°C. They were dehydrated through a graded ethanol series to 100% ethanol, which was replaced through a graded series with 100% propylene oxide (PO). Slow infiltration of Spurr's resin involved the following steps: 1) 24 hours in 25% (v/v) Spurr's resin in PO, 2) 36 hours in 50% (v/v) Spurr's resin in PO, 3) 48 hours in 75% (v/v) Spurr's resin in PO, 4) two 24-hour changes of 100% Spurr's resin. After a third change of resin, the specimens were placed in molds and cured for 24 hours at 65 °C. Thin sections were poststained for five minutes each with 2% uranyl acetate and basic lead citrate and viewed on a Hitachi H500 TEM.

MOLECULAR METHODS—DNA from the axenic culture of *Phaeoceros proskaueri* (Doyle 11,339) was extracted, amplified, and sequenced for the chloroplast gene *rbcL* (GenBank EU283415), following the protocol given in Forrest and Crandall-Stotler (2004). Additional hornwort *rbcL* sequences were downloaded from GenBank and manually aligned in PAUP* 4.0b10 (Swofford, 2002). The GenBank numbers for these sequences are given in Figure 7. The resulting matrix comprised 32 taxa and 1135 included characters, of which 354 were variable and 228 were

parsimony-informative. Maximum parsimony analyses were run in PAUP* under Fitch parsimony, with 10,000 random addition replicates, saving 25 trees per replicate. Eight most parsimonious trees were found, with a length of 541 steps. Bootstrap (BS) analysis was performed with the use of a heuristic search strategy, with 1000 replicates, each with 25 random addition replicates and saving no more than 25 trees per replicate. Maximum likelihood was implemented in GARLI 0.951 (www.bio.utexas.edu/faculty/antisense/garli/Garli.html; Zwickl, 2006) with 200 BS replicates and the General Time Reversible model (Yang, 1994) with a gamma rate distribution, which was selected as the best fit to the data by Duff et al. (2007). Three independent runs with the default parameters were used to identify the likeliest topology; each run found the same tree (Fig. 7) with Ln -46331.27762. The resulting tree was rooted on *Leiosporoceros dussii* (Steph.) Hässel, following its sister placement to all other hornworts in Duff et al. (2007).

Morphological Treatment

Morphological evidence unambiguously supports the recognition of three species in the problematic *P. hallii* group—*P. hallii*, *P. pearsonii*, and *P. proskaueri*, a new species named herein. All three are endemic to the Pacific Coast of North America, with *P. hallii* and *P. pearsonii* being broadly distributed from Washington to southern California and *P. proskaueri* known to date only from California. They occupy comparable habitats, sometimes even forming contiguous patches in a single locale, and have rather similar facies. Their elongate, more or less strap-shaped thalli bear abundant lateral or terminal tubers that typically persist on the soil surface. In contrast to *Phymatoceros*, which is sometimes intermixed with one or more of these species, the tubers are never ventral in position and rarely become deeply buried by the downward growth of a subtending stalk. A number of features separate them, as a group, from more widely distributed elements of the *P. laevis* (L.) Prosk. complex, the most consistent of which are seen in distal spore wall ornamentation. In the *P. hallii* group, the distal spore face bears a species-dependent, variable number of elongate, rounded ridges and/or mammillae, but in the *P. laevis* group, the distal spore face is spinose. The proximal spore face in both groups can be finely

vermiculate, often with clustered or scattered papillae. Spore morphology, as well as many other characters, also clearly separates *P. hallii* from *Paraphymatoceros* (Table 1). Although there are traits that suggest close affinity among the species of the *P. hallii* complex, each of them possesses a unique assemblage of characters, as detailed below.

PHAEOCEROS HALLII (AUSTIN) PROSK.—*Phaeoceros hallii* grows in moist, shaded habitats, over rocks in creeks or cascades, or on soils that are slow to dry, as in seeps or along creek banks, often mixed with grass, mosses, or both. As exemplified by the lectotype and paratype specimens of *A. hallii* (Hall 26 & 35, respectively) and *A. sulcatus* (Hall 25), thallus form is dependent on the moisture level of the habitat, a fact that likely influenced Austin (1875) to name two species. Specimens referred to *A. hallii* by Austin (1875) have elongated, flattened thalli with numerous tubers terminating most of the branch apices; fertile plants from the Silverton locality (Hall 26) bear 1 or 2 sporophytes at the thallus apices. The presence of diatoms on the thalli confirms that these plants were growing in very wet habitats, as indicated also by the notations, “springy places,” “dripping rocks,” or “cascades” on the packets. In contrast, the type specimens of *A. sulcatus* growing “on moist earth, Salem, Oregon,” (Austin, 1875: 27) have much shorter, somewhat thicker thalli that bear very few tubers and are crowded with short sporophytes. Indeed, most populations of *P. hallii* express this latter morphology. Except for these differences in thallus form, which appear to be environmentally induced, the type specimens of *A. hallii* and *A. sulcatus* are anatomically identical and referable to a single species as originally proposed by Howe (1898). This includes the sterile specimens on dripping rocks (Hall 35), which Howe (1898: 11) mistakenly suggested were likely his new species, “*A. pearsoni*.”

Thalli are caespitose as they germinate from the dormant tubers but become more or less prostrate and intertwined in irregular mats with continued growth. They are linear, 1.3–3.0 mm in width, and irregularly branched, with the branches narrower than the main axis. Late in the growing season, dorsiventrally flattened, orbicular, dark green to blackish tubers, to 1.5 mm in diameter, terminate many of the lateral branches, as well as the main axes of thalli without sporophytes (Fig. 1.2, Table 1). As the plants dry, the wing margins inroll, imparting what Howe (1898: 10) described as a “plicate-costate” appearance to the thallus.

TABLE 1. Morphological features of the *Phaeoceros hallii* complex and *Paraphymatoceros diadematus*. Items marked with an asterisk (*) were taken from Hässel de Menéndez (2006).

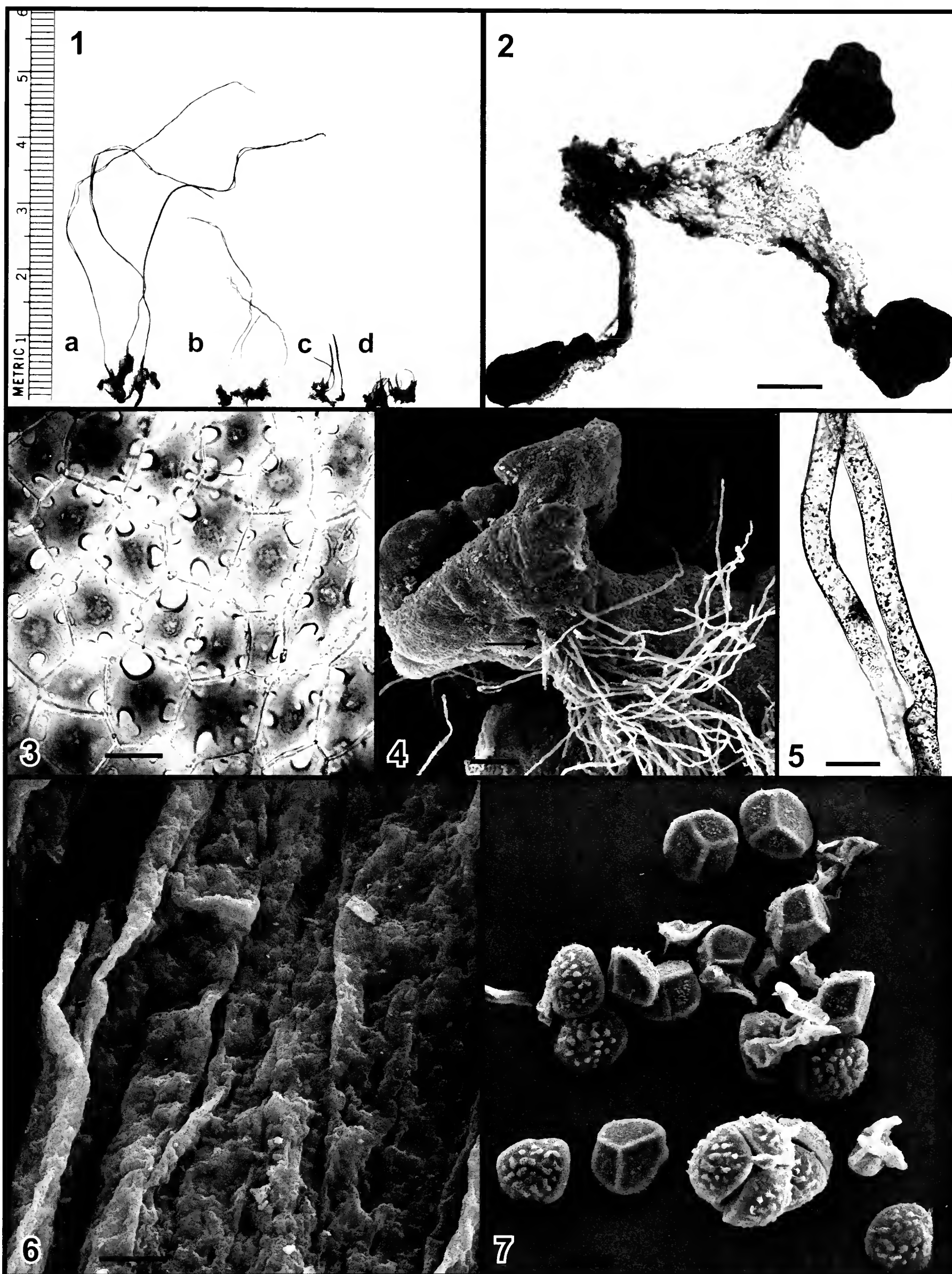
Taxon/Character	<i>Phaeoceros proskaueri</i>	<i>Phaeoceros hallii</i>	<i>Phaeoceros pearsonii</i>	<i>Paraphymatoceros diadematus</i>
Thallus width	Males 0.3–0.8 mm; females 1.5–2.0 mm	1.3–3.0 mm	2.5–5.0 mm	0.7–3.0 mm
Thallus margin	2-stratose, abrupt constriction	3 or 4-stratose, abrupt constriction	2 to 4-stratose, gradual taper	1-stratose, gradual taper
Plastid structure	Spheroidal to spindle-shaped; pyrenoid absent	Plate-like to spindle-shaped; pyrenoid present	Spheroidal to plate-like; pyrenoid absent	Pyrenoid absent*
Tuber morphology	Terminating “dwarf” lateral branches; subspheroidal, rarely flattened, < 1 mm	Terminating apices, flattened, to 1.5 mm	Marginal or apical, flattened, to 2.5 mm	Submarginal–ventral, flattened, to 2.0 mm
Sexuality	Dioicous, dimorphic	Monoicous, weakly protandrous	Monoicous, strongly protandrous	Dioicous*
No. of antheridia/chamber	1	2 to 4	1	4 or 5*
Capsule length (cm)	0.7–1.75 cm	0.4–0.6 cm	2.0–4.0 cm	4.8–7.0 cm
Columella	Rigid, brown	Flaccid, hyaline	Rigid, brown	Rigid, brown
Spore Maturation	Nonsynchronous	Synchronous	Nonsynchronous	Nonsynchronous
Dehiscence	1 longitudinal slit, valves adherent at the apex	Indehiscent, or with 1 short slit; valves adherent at the apex	1 longitudinal slit, slightly twisted; rarely 2-valved; valves adherent at the apex	2-valved, helically twisted; apically free
Spore color at dehiscence	Deep brown to fuscous	Bright yellow to yellow-orange	Tawny to light blackish brown	Tawny to medium blackish brown
Pseudoelaters in median part of capsule	Brown, mostly 2- or 3-celled, to 110 µm long	Pale yellow to tan, mostly 1-celled, <60 µm long	Brown, 3- or 4-celled, to 200 µm long	Blackish brown, 3- or 4-celled, to 400 µm long

The main axis is 6 to 9 cells thick for most of its width, narrowing abruptly to 3 or 4 cells in thickness within 100 µm of the thallus margin. Internal cells are thin-walled, isodiametric, and 35–48 µm in diameter, with slightly larger mucilage cells dispersed among them. Cells of the dorsal epidermis are rhombic pentagonal to hexagonal (rarely quadrate) and 38–46 µm in diameter, with cells near the thallus midregion, elongated to twice their width (Fig. 1.3). Each dorsal epidermal cell bears a single, pleomorphic plastid that can assume a flattened, amoeboid-like outline, or become spindle-shaped to spheroidal, depending on environment. Ventral epidermal cells, which are smaller than the dorsal cells, averaging 25 µm

in diameter, typically have only spindle-shaped to subspheroidal plastids, as do all cells of immature thalli grown in axenic culture and cells of developing tubers. A spheroidal pyrenoid-like zone of starch grains is clearly visible in the center of each plastid in the amoeboid or spindle phases (Fig. 1.3), but not in the subspheroidal phase, at least in optical microscopy. Although this structure resembles the pyrenoids of the *P. laevis* complex, only ultrastructural studies can determine with certainty whether this region possesses pyrenoid organization or is simply a centralized aggregation of starch grains.

Rhizoids, which are abundant on thalli growing over soil, typically adhere to each other in

FIG. 1. *Phaeoceros hallii* (Austin) Prosk. 1. Comparison of sporophyte-bearing plants of *Paraphymatoceros diadematus* Hässel (a; from the holotype), *Phaeoceros pearsonii* (M. Howe) Prosk. (b; from Doyle 11415), *Phaeoceros proskaueri* Stotler, Crand.-Stotl. & W. T. Doyle (c; from Doyle 7268) and *P. hallii* (Austin) Prosk. (d; from Doyle



8445), all natural size. **2.** Portion of a thallus with terminal tubers (1-mm scale). **3.** Surface view of the dorsal epidermis, showing cells with irregularly shaped plastids, with central pyrenoids (30- μ m scale). **4.** SEM of a chemically preserved thallus, ventral view, showing clumped, adherent rhizoids at the arrow (250- μ m scale). **5.** Granulate rhizoids, viewed with a compound microscope (35- μ m scale). **6.** SEM of a group of air-dried, adherent, granulate rhizoids (8- μ m scale). **7.** SEM of spores and pseudoclasts (30- μ m scale). [2 from Doyle 11390; 3, 5 from Doyle 11366; 4 from Doyle 11363; 6 from the lectotype of *A. hallii*; 7 from the lectotype of *A. sulcatus*]

bundles or plate-like masses (Fig. 1.4). They are up to 20 μm in diameter, pale brown, and densely granulate in transmitted light (Fig. 1.5), an attribute noted by Austin (1875) as diagnostic of *A. sulcatus*. In addition, smooth, narrower, nonfascicled rhizoids are also present, especially on young thalli and near thallus apices. Although granulate—bundled rhizoids are a striking feature of *P. hallii*—we have observed similar rhizoids, sometimes intermixed with rhizoids that are smooth walled, or nongranulate, in many other hornworts, including other species of *Phaeoceros*, *Notothylas*, *Paraphymatoceros*, and *Phaeomegaceros* Duff et al. Transverse sections of these distinctive rhizoids demonstrate that the granular appearance is due to deposits on the inner surface of the rhizoid cell wall, much like the tubercles or pegs of pegged rhizoids in complex thalloid liverworts. As a consequence, in SEM micrographs, the outer wall of the rhizoid appears smooth in noncollapsed, chemically fixed material (Fig. 1.4), but irregularly roughened in air-dried material in which surface wall collapse exaggerates the inner, noncollapsed deposits (Fig. 1.6). Despite their widespread occurrence in hornworts, these granulate rhizoids have not been previously described. Schuster (1992) does indicate that the rhizoids of *Anthoceros* sensu R.M.Schust. (= *Phaeoceros*) are smooth or punctate (p. 743) and those of *Aspiromitus* Steph. sensu R.M.Schust. (= *Anthoceros*) are smooth or weakly roughened (p. 781), without further discussion, but most authors describe hornwort rhizoids as unicellular and smooth (e.g., Renzaglia & Vaughn, 2000).

As first reported by Howe (1898), *P. hallii* is monoicous, and slightly protandrous. Antheridial chambers are frequently borne on different branches than the archegonia, with up to 6 chambers per branch, but can occasionally be observed on the main thallus, somewhat posterior to a cluster of developing sporophytes. The chambers are 350–400 μm in diameter and contain 2 to 4 antheridia. When mature, the rupture of the chamber roof forms a collar 2 to 4 cells high that persists around the chamber cavity.

Sporophytes are usually numerous, occurring in clusters near thallus apices (Fig. 1.1). Involucres are no more than a third the length of the capsules and are cylindrical, but with the mouth slightly flared. Capsules are erect to slightly bent, less than 6 mm long, and yellow to light brown when mature. Stomates are scattered throughout the

epidermis, frequently in pairs, with the guard cells brown in dried collections. In median transverse section, the capsule wall is 4 to 6(7) cells thick. The radial walls of the quadrate epidermal cells are thickened, the 2 to 4(5) layers of assimilatory cells are thin-walled, isodiametric, and 35–40 μm in diameter, and the innermost cells that line the spore sac are narrowly rectangular, averaging 8 μm in depth, with their inner tangential walls slightly thickened. A hyaline columella, consisting of up to 30 columns of elongate, fragile, thin-walled cells that collapse before spore release, extends the entire length of the spore sac. The spore sac ends 250–300 μm below the constricted, knob-like tip of the capsule.

Sporophytes of *P. hallii* resemble those of *Notothylas* in having growth from the basal meristem cease early in ontogeny, even though moisture conditions are suitable for continued growth. Sporogenesis is more or less synchronous, so mature spores fill the entire spore sac at capsule opening. With drying, the capsule shrinks, becomes longitudinally ridged and appears acutely 4-angled. Numerous undehiscent capsules, bulging with mature yellow orange spores, are present in most collections, which suggests that capsules are either nondehiscent or very slow to dehisce. In the few cases in which dehiscent capsules have been observed, a single longitudinal suture begins to open about a third of the way down from the capsule tip. The epidermal cells bordering the suture are narrower than the neighboring epidermal cells but are otherwise indistinguishable, and no clearly defined suture is visible in undehiscent capsules. Mature, undehiscent capsules frequently break off near their insertion in the thallus; this could allow for spore release and dispersal without dehiscence.

Spores are bright yellow to yellow-orange, anisopolar and 42–60(–63) μm in equatorial diameter. Both proximal and distal surfaces are covered with a matrix of fine, interwoven vermiculate thickenings. The distal face is additionally ornamented with 20 to 35 mammillae or short rounded ridges that are 3.5–4.0 μm in width and 3.0–3.5 μm in height (Figs. 1.7, 6.1–6.4). The proximal face has a distinct trilete ridge, and each triangular facet bears a central cluster of 20 to 30 (rarely fewer) papillae, 1.0–1.2 μm in diameter. In optical microscopy, the spore appears rimmed by a thin wing, or cingulum, more than 2.0 μm wide. Pseudoelaters are pale yellow to tan, 15–20 μm wide, mostly 1-celled and usually only slightly longer than broad (Fig. 1.7).

PHAEOCEROS PEARSONII (M. HOWE) PROSK.—As initially suggested by Howe (1898), thalli of *P. pearsonii* are quite variable in size and form, with smaller, more highly branched forms occupying drier, more exposed sites. Thalli are typically larger, rather crispate and more spreading than those of *P. hallii* (Fig. 1.1, Table 1), with thallus lobes up to 5 mm wide in robust forms. Individual thalli become flabellate with branching (Fig. 2.2), with branches near the apex diverging subdichotomously. The margin of the thallus is often irregularly crenate to shallowly incised, especially in plants bearing sporophytes. Flattened, elongate, dark green tubers, up to 2.5 mm in width and of variable length, are formed at the thallus apices as well as along the thallus margins (Fig. 2.1, 2.2). In contrast to the orbicular tubers of *P. hallii*, the tubers of *P. pearsonii* are irregular in outline, sometimes including an apical dichotomy and extending for some distance down the margin from the apex (see Howe, 1898: pl. 322). Tubers formed on thin branches can become descendent with downward growth of the branch, but most remain near the soil surface when the subtending thallus dies.

In transverse section, the thalli gradually taper from 6 to 11 cells thick in the middle to 2 to 4 cells thick near the margin, with a single cell projecting at the thallus margin proper. In general, thalli growing in more exposed habitats comprised more cell layers than those from shaded habitats. Interior cells are elongate, 38.5–42.0 μm wide \times 65–75 μm long, and larger and more vacuolate than the epidermal cells. Mucilage cells are widely scattered throughout the thallus. Cells of the dorsal epidermis are rhombic to elongated, 19–28 μm in diameter, and up to 70 μm long. The single large plastid in each dorsal epidermal cell is orbicular to angled and internally homogeneous, lacking a pyrenoid (Fig. 2.3), as also reported by Bartlett (1928) and Duff et al. (2007). Indeed, this difference in plastid structure immediately differentiates thalli of *P. pearsonii* from those of *P. hallii*. Cells of the ventral epidermis sometimes have 2 orbicular plastids, or plastids that are dumbbell-shaped, and interior cells of the midrib occasionally have 4 plastids (Bartlett, 1928; Doyle & Stotler, 2006).

Rhizoids are both nongranulate and granulate, with a fairly equal mix of both on any thallus. They are hyaline, fairly abundant on older parts of the thallus, and never fasciculate or adherent.

Plants are monoicous, but exceedingly protandrous. Antheridial chambers begin development with the initiation of tuber germination,

sometimes forming even within the fleshy tissue of the tuber (Howe, 1898: pl. 322). As the thallus expands out from the tuber, successive rows of antheridial chambers are formed (Fig. 2.4). The chambers are spheroidal, 100–120 μm in diameter and house a single antheridium per chamber (Fig. 2.5). The chamber collar is 2 to 4 cells high and 2 cell layers thick at the base. Archegonia are formed much later in tuberling germination, after maturation and dehiscence of the antheridia on that thallus. In a natural population, some tuberlings would be producing antheridia and others archegonia, thus facilitating fertilization among tuberlings. This does not preclude self-fertilization, however, in that many tubers within a population could have been formed on the same parent thallus. We have not observed empty antheridial chambers on live thalli with mature sporophytes but have observed antheridial production on germinating tubers that are still attached to dead remnants of sporophyte-bearing thalli.

Sporophytes occur singly or in pairs near the thallus apex (Fig. 1.1b). Involucres are up to 5 mm long and narrowly cylindrical, with the mouth entire and appressed to the capsule, never flared as in *P. hallii*. Capsules with nearly mature to mature spores are tan to dark brown and range from 2 to 4 (rarely 5) cm in length, with longer capsules occurring in slower to dry habitats. Of course, length also varies with the time of collection, in that in nature, the basal meristem will continue to generate cells, even after mature spores are present at the capsule apex; thus, capsules collected in late March tend to be shorter than those collected nearer the end of the growing season in June. Stomates are dispersed throughout the epidermis. In the median part of the capsule, the wall consists of an epidermis, 3 layers of plastid-containing, assimilatory cells, and an inner “endodermis-like” layer. The radial walls of the epidermal cells are pigmented and thickened, as also are the radial and inner tangential walls of the endodermis-like layer. The columella consists of 16 columns of thick-walled cells and is visible as a smooth, rigid, pale brown to dark brown central strand at capsule dehiscence. Most capsules dehisce along a single longitudinal suture that begins just below the solid apical knob of the capsule and extends basally, but dehiscence along 2 sutures can also occur. The suture cells are narrower than the surrounding epidermal cells and unpigmented. When the capsule opens along 2 sutures, the split along one of them is often

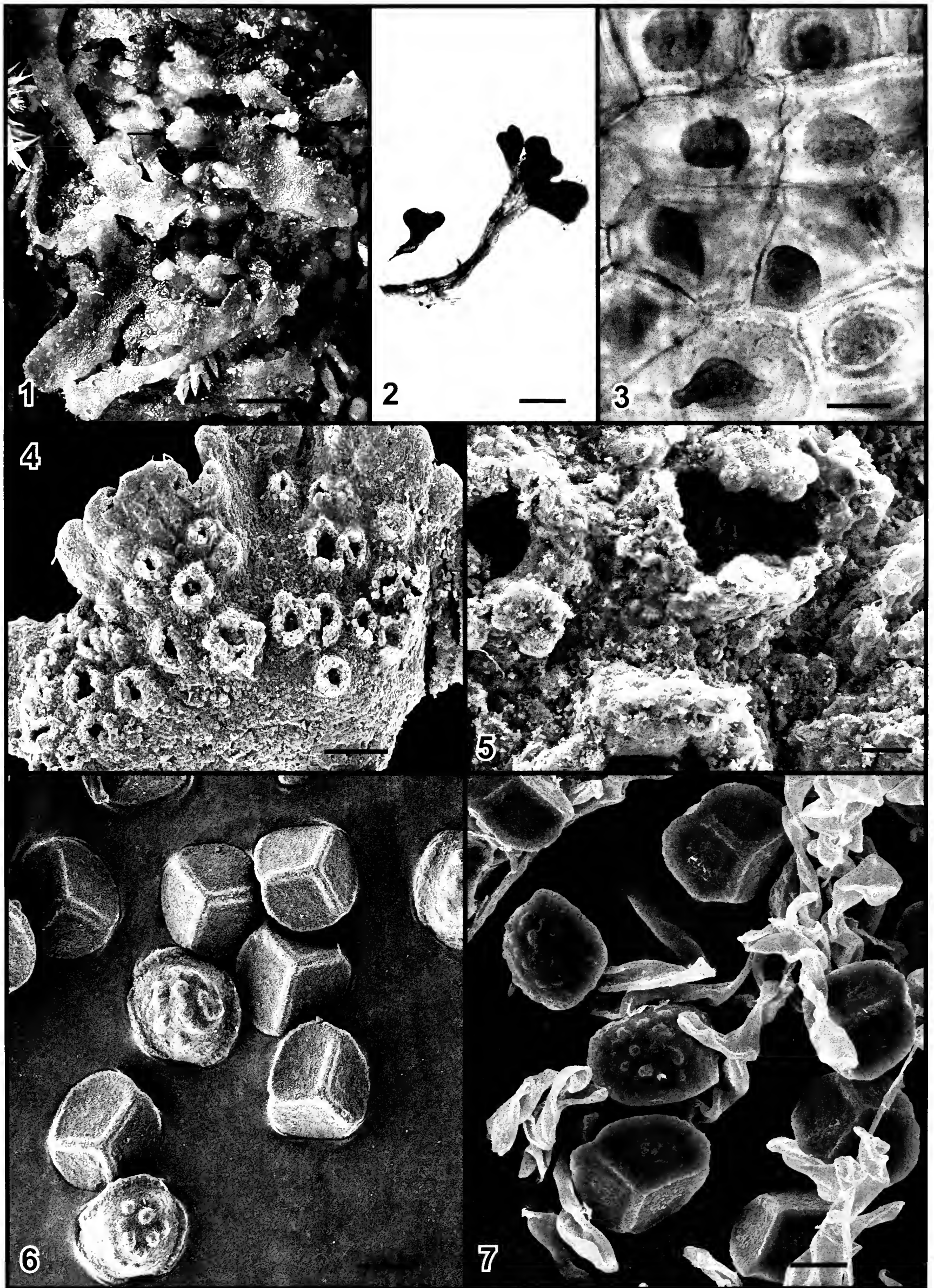


FIG. 2. *Phaeoceros pearsonii* (M. Howe) Prosk. 1. Habit of young tuber-bearing plants, showing tubers in both lateral (at arrow) and apical positions (2-mm scale). 2. Thalli showing apical and marginal tubers (3-mm scale). 3. Surface view of the dorsal epidermis, showing plastids that lack pyrenoids (14- μ m scale). 4. SEM of a thallus soon after its emergence from a tuber, showing numerous rows of antheridial cavities (100- μ m scale). 5. Antheridial cavity with a single antheridium, SEM (50- μ m scale). 6. SEM of spores that are characteristic of the species (20- μ m scale). 7. SEM of spores and pseudoelaters that are light blackish brown and bear a few proximal facet papillae (20- μ m scale). [1 from Doyle 11325; 2, 3 from Wagner m2269; 4, 5 from Doyle 11420; 6 from Doyle 8423; 7 from Wagner m1387]

incomplete. In nature, the valves remain adherent at the apex and slightly twisted.

Sporogenesis is nonsynchronous, so even though a capsule is dehiscent, not all spores in it are mature. Fully mature spores in field-dried specimens are usually yellow to tawny, anisopolar and 36–48 μm in equatorial diameter (Fig. 2.6). They resemble the spores of *P. hallii* in having both proximal and distal surfaces covered with a matrix of fine, interwoven vermiculate thickenings. The distal surface is further ornamented with 5 to 15 mammillae or rounded, crescentic projections, but the facets of the proximal face are generally otherwise unornamented. There is a prominent trilete ridge on the proximal face, and a distinct wing or cingulum. In optical microscopy, the proximal facets appear granulose as Howe (1898) described them. Isotype specimens of both *A. pearsonii* [CA] and *A. bolanderi* Steph. [CA] exhibit this pattern of spore wall architecture (Fig. 6.5–6.8), supporting the proposal by Hässel de Menéndez (1989) that they are conspecific. Although most populations possess spores of this type, in a few geographically dispersed populations, mature spores in field-dried capsules develop a blackish brown pigmentation that obscures the vermiculate thickenings and possess a few central papillae on some, or all, of the facets of the proximal face (Figs. 2.7, 6.11, 6.12). This spore morphology seems to occur more frequently in populations growing in exposed habitats (Doyle & Stotler, 2006) but does not define all such populations. Plants with this spore morphology are totally referable to *P. pearsonii* in all other features, leading us to conclude that spore characters by themselves are not always reliable indicators of taxon identity, a conclusion also reached by Proskauer (1957) for the *P. laevis* complex.

Pseudoelaters are brown, 8–12 μm wide, and 3 or 4 cells long in the median part of the capsule or spore tetrad zone. In the zone of spore maturation, the pseudoelaters fragment, so when dispersed, they are typically only 1 or 2 cells long. Individual cells can be up to 80 μm long.

PHAEOCEROS PROSKAUERI STOTLER, CRAND.-STOTL. & W. T. DOYLE, SP. NOV.—This previously undescribed, tuberous species has been collected from numerous localities in California, including the western foothills of the Central and Southern Sierra Nevada and the coastal ranges of the South and Central Coast Regions. It is most common on disturbed, fine-grained soils that dry soon after the end of the winter–spring rains, such as exposed

areas on hillsides, abandoned dirt roads, road cuts, trail banks, banks of ephemeral creeks, openings in the chaparral, or among oaks. It sometimes grows with *P. pearsonii*, *P. bulbiculosus*, and *A. fusiformis*, as well as various species of *Asterella* P. Beauv., *Fossombronia* Raddi, *Riccia* L., *Sphaerocarpos* Boehm., and *Targionia* L.

In contrast to both *P. hallii* and *P. pearsonii*, thalli of *P. proskaueri* are unisexual and highly dimorphic, with tuberling populations typically consisting of contiguous clusters of male and female plants (Fig. 3.1, 3.6). Tuber germination occurs in late fall to early winter, shortly after the onset of the rainy season. Soon after emergence from the tubers, male thalli measure less than 400 μm in width, whereas developing female thalli in the same population are more than 900 μm wide. As development continues, thallus segments on male plants reach a maximum width of 800 μm , and those of female plants enlarge up to 2.0 mm in width. Male plants are much more highly branched than females and bear more abundant tubers (Fig. 3.1, 3.2). The tubers are distinctive. They are usually subspheroidal and only slightly dorsiventrally flattened, occasionally more elongate and flattened, and develop mostly at the apices of abundantly produced, very short lateral branches. In early stages of tuber development, these short branches look like quadrate lobes of an incised thallus margin (Fig. 3.1), but they bear apical cells and can grow into normal, elongate lateral branches if tuber formation does not occur. During tuber formation, the apical cell of the branch no longer functions, and the whole branch becomes thickened. Although these tubers can look like they are marginal, they do not originate from marginal cells of the thallus. Tubers formed in this way develop early in the growing season; they are initially pale green, but with the deposit of pigments in the epidermal cell walls, are brown at maturity. Internal tissues are achlorophyllose, test negative for starch, and contain oil droplets and small protein granules. Near the end of the growing season, the apices of leading thallus segments may also become tuberous. In contrast to the early-formed lateral tubers that persist on the soil surface, these apical tubers tend to be more elongate and are sometimes pushed downward by the elongating thallus tissue behind them.

The thallus is differentiated into a broad central midrib, which bears the rhizoids, and thinner wings. In transverse section, the midrib is 10 to 16

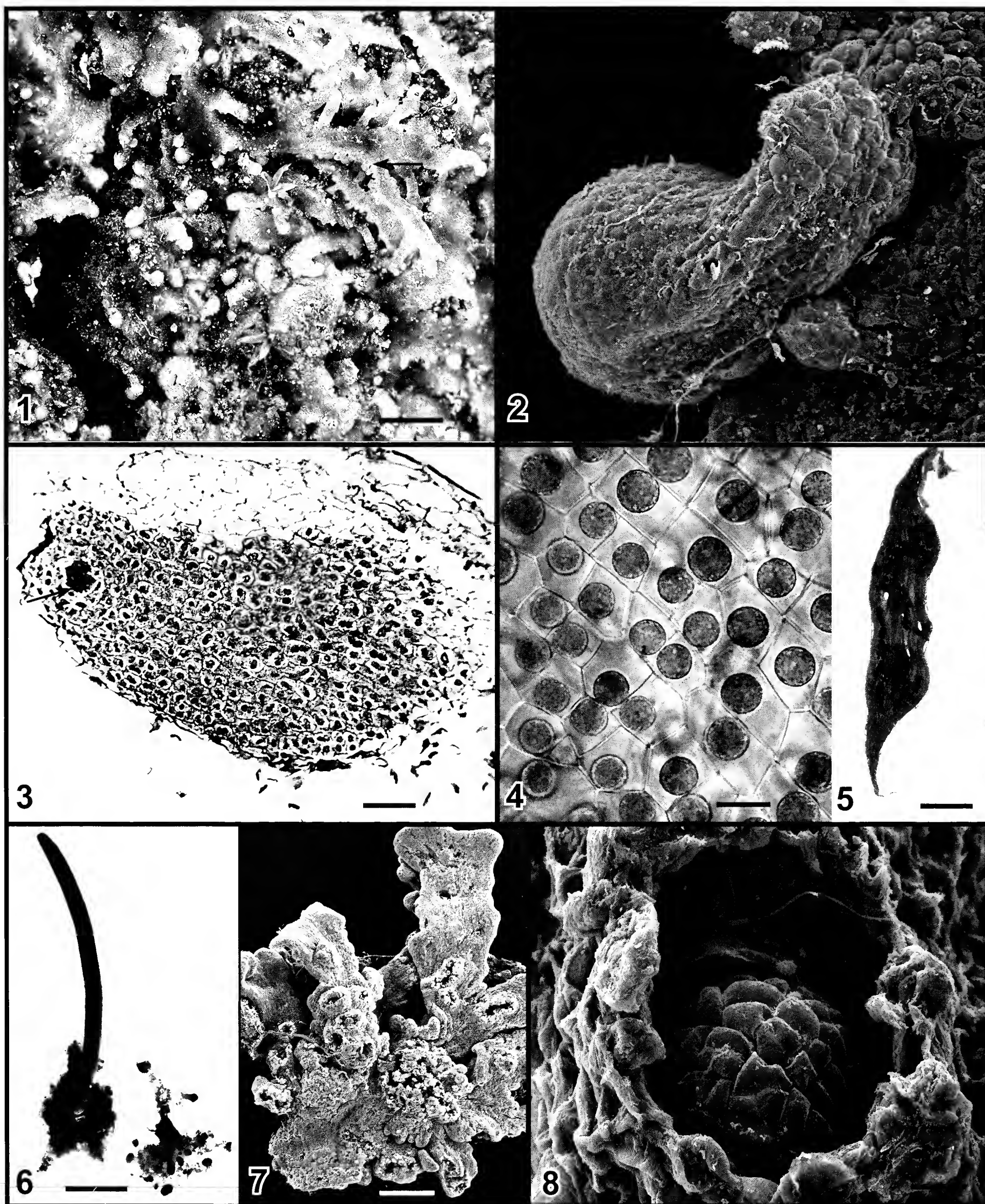


FIG. 3. *Phaeoceros proskaueri* Stotler, Crand.-Stotl. & W. T. Doyle. 1. Habit of young tuber-bearing plants, showing very short lateral branches beginning to form tubers at their apices (at arrow) (1.5-mm scale). 2. SEM of a typical tuber (75- μ m scale). 3. Vertical longitudinal section through a developing tuber; the apical cell and meristematic tissues of the young branch are still present, indicated by arrow (60- μ m scale). 4. Surface view of the dorsal epidermis, showing plastids that lack pyrenoids (20- μ m scale). 5. TEM of a single plastid, showing small peripheral starch grains and no pyrenoid (2.6- μ m scale). 6. Mature thalli, male (on the right) and female (on the left), showing the dimorphism of the sexes (2-mm scale). 7. SEM of a male plant soon after emergence from the tuber, remnants of which are in the lower left (525- μ m scale). 8. Antheridial cavity with a single antheridium (25- μ m scale). [1, 3 and male plant in 6 from Doyle 11357; 2 from Doyle 11328; 4, 7, 8 from Doyle 11431; 5 and the female plant in 6 from Doyle 11339]

cells thick and constricts abruptly to the wings, which are 4 to 10 cells thick. Near the thallus margins, the wings taper to 2 cells in thickness. This thinner area of the wing margin turns upward when the thallus dries. A few scattered mucilage cells, as well as the *Nostoc* colonies, are restricted to the midrib. There is no consistent difference in thallus thickness between males and females, but the wing portion of the thallus is much narrower in male plants so the midrib occupies a larger proportion of the thallus. Interior cells of the midrib are longitudinally elongated, 30.4–38.0 μm in diameter and up to 120 μm in length; interior cells of the wing are similar in size, but are radially elongated. Both dorsal and ventral epidermal cells are quadrate in transverse section, 20–30 μm in diameter, with dorsal cells rhombic pentagonal or rectangular in surface view (Fig. 3.4). Plastids are orbicular in surface view, but oval to spindle-shaped in section and definitely lack pyrenoids (Fig. 3.5). Small, dispersed starch grains and strands of osmiophilic spherules are within the plastid matrix.

Rhizoids are abundant on the thallus midrib and are mostly of the granulate type, with non-granulate rhizoids occurring only near the thallus apex and on developing tubers. Although granulate, the rhizoids are hyaline and never adherent or fascicled as in *P. hallii*.

Male thalli dichotomize right after emergence from their tubers. The two branches grow unequally, with one remaining small and close to the tuber and the other expanding to form the major axis of the plant. As in *P. bulbiculosus* (Crandall-Stotler et al., 2006), antheridial chambers form very soon after tuber germination, occurring in clusters at the base of both branches (Fig. 3.7). Individual chambers are broadly cone-shaped, 200–300 μm across at the base, and elevated above the thallus surface even before opening. Each contains a single antheridium (Figs. 3.8, 4.1). Mature antheridia are yellow-orange, up to 200 μm in diameter, with untiered jacket cells and a 4-seriate stalk, up to 3 cell rows in length. The chamber collar, formed from the roof cells of the chamber, is hyaline and up to 5 cells high. Sometimes, the opening of contiguous chambers produces a single collar, giving the appearance of a single elongate chamber with 2 antheridia. The presence of an internal partition between the antheridia, however, verifies that all chambers are developmentally monandrous. After a short period of antheridial production, the male thalli undergo a period of vegetative

growth, with extensive branching and tuber production. The antheridial chambers, which are produced only near the base of the male thallus, deteriorate early in the growing season, long before the maturation of sporophytes on the female thalli, and hence are not preserved in most herbarium collections.

Female plants undergo a small amount of vegetative growth after tuber emergence, dichotomizing at least twice before producing archegonia at their broadened thallus apices. At the time of fertilization, female thalli are typically less than 1.0 mm in width, but still almost 3 times as large as male thalli in the same population. As sporophytes develop, the thalli grow in length and width and initiate the short tuber-forming branches. Tubers are fully developed by the late stages of sporophyte maturation.

Sporophytes occur singly or rarely in pairs at the apices of the female thallus lobes. They are substantially larger than those of *P. hallii*, but much smaller than those of *P. pearsonii* (Fig. 1.1c). The involucre is short, 0.6–1.5 mm high, and narrowly campanulate, with the mouth flared to 0.7 mm wide. Capsules are usually less than 1.0 cm long, but can be up to 1.75 cm in sites where moisture is available later into the season. The capsule wall consists of an outer epidermis, three layers of plastid-containing assimilatory cells and an inner “endodermal” layer (Fig. 4.2). The radial walls of both the epidermal and inner “endodermal” cells are darkly pigmented and thickened. The columella consists of 16 columns of thick-walled, elongate cells and, as in *P. pearsonii*, is visible as a rigid, brown central strand in dehiscing capsules. Stomates occur singly and are scattered throughout the epidermis. Field-matured capsules are blackish brown at the tip, to brown in the median zone of still maturing spores. They open along a single longitudinal suture that is visible as a line of yellow to orange cells, extending basally from just below the knob-like tip of the capsule. In capsules that dehisce when less than 7 mm long, the valves and dehiscence slit are straight, but in longer capsules they are helically twisted.

Sporogenesis is nonsynchronous. Spores that have just emerged from tetrads in the median to basal part of mature capsules are partially covered with remnants of the sporocyte wall and intrasporal septum (Fig. 4.3). Slightly anterior to the tetrad zone, these remnants are no longer visible, and a matrix of vermiculate thickenings can be seen covering both proximal and distal

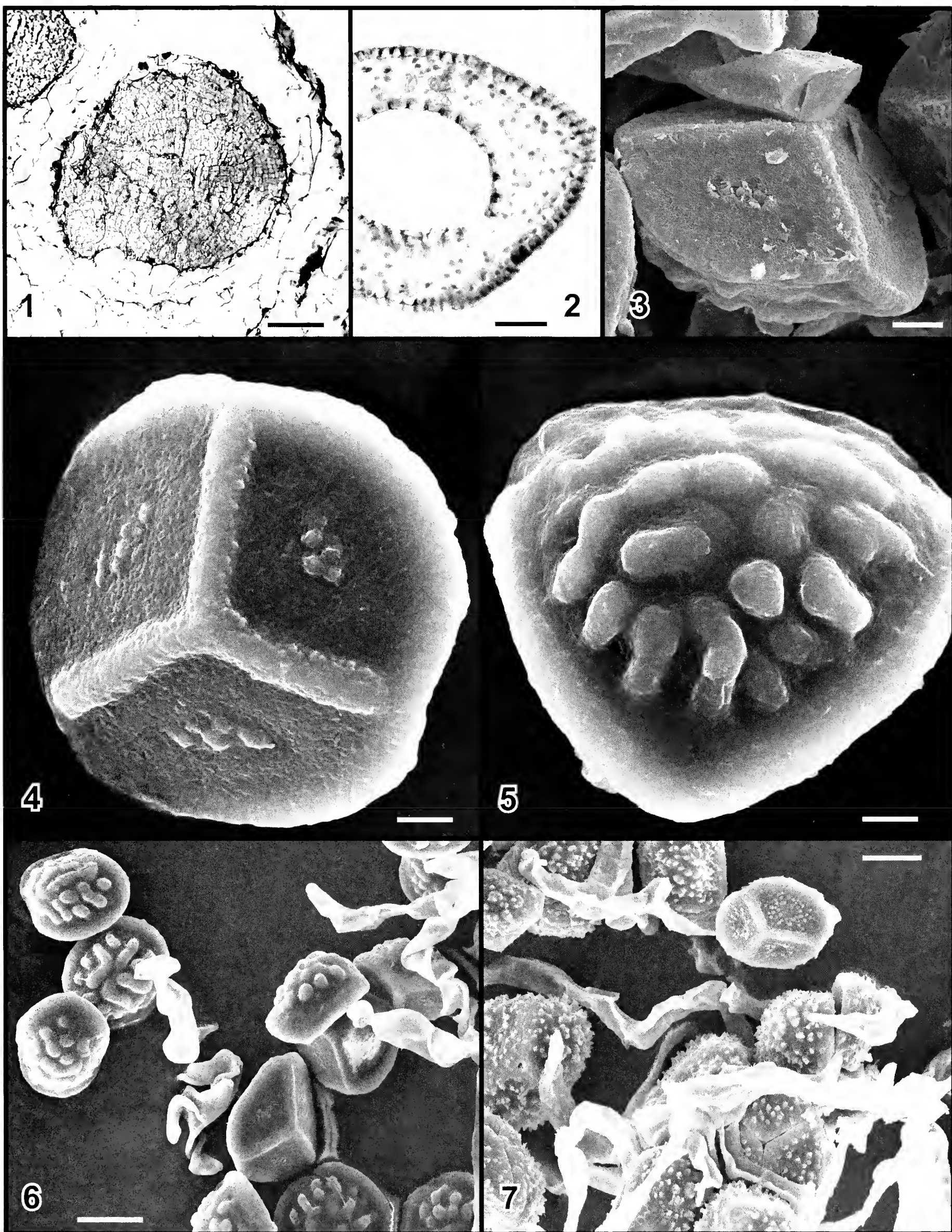


FIG. 4. *Phaeoceros proskaueri* Stotler, Crand.-Stotl. & W. T. Doyle (1–6) and *Phaeoceros tuberosus* (Taylor) Prosk. (7). 1. Vertical longitudinal section through a single antheridial chamber (50- μ m scale). 2. Transverse section through capsule wall (150- μ m scale). 3. SEM of spore that has just separated from its tetrad; note the remnants of the intrasporal septum and the densely vermiculate spore wall thickenings beneath it (10- μ m scale). 4, 5. SEM of proximal (4) and distal (5) faces of mature deep brown spores from field-dehiscid capsules (5- μ m scale). 6. SEM of dispersed spores and pseudoelaters from near the capsule apex (20- μ m scale). 7. SEM showing spores, spore tetrads and pseudoelaters (20- μ m scale). [1 from Doyle 11422; 2, 4–6 from Doyle 11339; 3 from Doyle 11328; 7 from the lectotype]

faces of the spores, which at this stage are yellow to tawny. The proximal face bears a distinct trilete ridge and a small central cluster of 4 to 10 papillae, 2.5–3.0 μm in height (Figs. 4.4, 6.10). The distal face is conspicuously ornamented with 13 to 30 rounded mammillae or elongate, rounded ridges, 5.0–6.0 μm in diameter, and a cingulum, or wing, is present (Figs. 4.5, 6.9). At this stage, the spores bear some semblance of the spores of *P. hallii*. In fully mature capsules that dehisce in the field, however, spores at the capsule apex are deep brown to fuscous, and the vermiculate matrix of the spore surface is obscured (Fig. 4.4, 4.5). Such fully mature spores are smaller than those of *P. hallii*, 36–49 μm in diameter. As in *P. bulbiculosus*, there appears to be a deposition of some type of coating material over the spore wall during the final stages of spore maturation (Crandall-Stotler et al., 2006). This late modification of spore wall structure never occurs in *P. hallii*, but does occur to a limited extent in a few atypical populations of *P. pearsonii*. Spores of the latter are, nonetheless, distinguished from those of *P. proskaueri* in having fewer mammillae on the distal face and more widely dispersed, smaller proximal face papillae (Fig. 6.11, 6.12).

Pseudoelaters are brown and 2 or 3 cells long in median parts of the capsule, but fragment into 1(2)-celled structures near the capsule apex. Individual cells are 12–18 μm wide and up to 40 μm long.

Clearly, *P. proskaueri* is morphologically distinct from all other tuber-producing hornworts common to western North America (Table 1). It is also decidedly different from *Phaeoceros tuberosus* (Taylor) Prosk. (= *Anthoceros tuberosus* Taylor), a species distributed in western Australia, and *P. diadematus* Hässel, a newly described taxon from Chile (Hässel de Menéndez, 2006). The lectotype collection of *A. tuberosus* is dioicous and dimorphic, with male thalli up to 1.5 mm wide and female thalli to 2.8 mm wide. Small tubers, less than 0.4 mm in diameter, are formed, sometimes abundantly, at the apices of elongate lateral branches. They are never ventral in origin as described by Ashworth (1896), and except for their much smaller size, resemble the tubers of *P. hallii*. The few male plants in the collection bear groups of empty antheridial chambers near the tips of elongate thallus lobes. Sporophytes are 1.0–1.3 cm long, yellow to brownish orange, and possess stomates in the capsule wall. Capsule dehiscence occurs along 2 sutures that are straight to slightly twisted. The spores are yellow to yellow

orange, even at the tips of completely opened capsules, and are covered with a dispersed network of vermiculate thickenings. The proximal surface bears a prominent trilete ridge and up to 30 dispersed papillae on each facet; the distal surface bears numerous conical verrucae that are 3–4 μm high (Fig. 4.7). Pseudoelaters are pale yellow, mostly 3- or 4-celled and often branched. This assemblage of characters suggests that the affinities of *P. tuberosus* lie with *P. laevis*, not the *P. hallii* complex.

According to Hässel de Menéndez (2006), *P. diadematus* is also a dioicous taxon. Males are described as having 4 or 5 antheridia per antheridial cavity (Hässel de Menéndez, 2006), but we were unable to find antheridial chambers in the specimens we examined, including the type. In two of the collections, we did find two size classes of thalli, suggesting that the sexes are dimorphic. Thalli with immature sporophytes range from 1.5 to 1.9 mm in width, whereas those in the same collection without sporophytes are 0.7–0.8 mm in width. Collections bearing these smaller thalli were made in late August (*Villigrán 1017*) and mid-September (*Villigrán 1029*), whereas the holotype (*Villigrán 1115*), which bears mature, dehiscent capsules, was collected in early November. The maximum width of sporophyte-bearing thalli in this latter collection is 3.0 mm. Thalli are very thin, 3 to 4 cells thick at the thallus midline, tapering to only 1 cell thick within 6–8 cells of the thallus margin. We have not studied live material, but Hässel de Menéndez (2006) reports that the chloroplasts lack pyrenoids and occur singly in the cells. Rhizoids are granulate, sometimes adherent in plate-like masses, and 12–19 μm in diameter; they frequently have broadly flared, funnel-shaped tips. In the *P. hallii* complex, the rhizoids are always bluntly rounded at their tips, never flared, but we have observed similar flared rhizoids in species of *Phaeomegaceros*.

Tubers are formed ventrally from submarginal cells near the dichotomizing apical notch of the main thallus, at other points along the thallus border, or at the tips of elongate lateral branches (Fig. 5.1). The thallus margin extends dorsally beyond the tuber by 2 or 3 cells. Tubers are elongate, to 2.0 mm long and 1.0 mm wide, dark brown at maturity, and covered with rhizoids ventrally. They are never stalked or descendent.

Capsules in the holotype are dark brown, up to 7.0 cm long and dehiscent for about two-thirds their length (Fig. 1.1). They are split along two

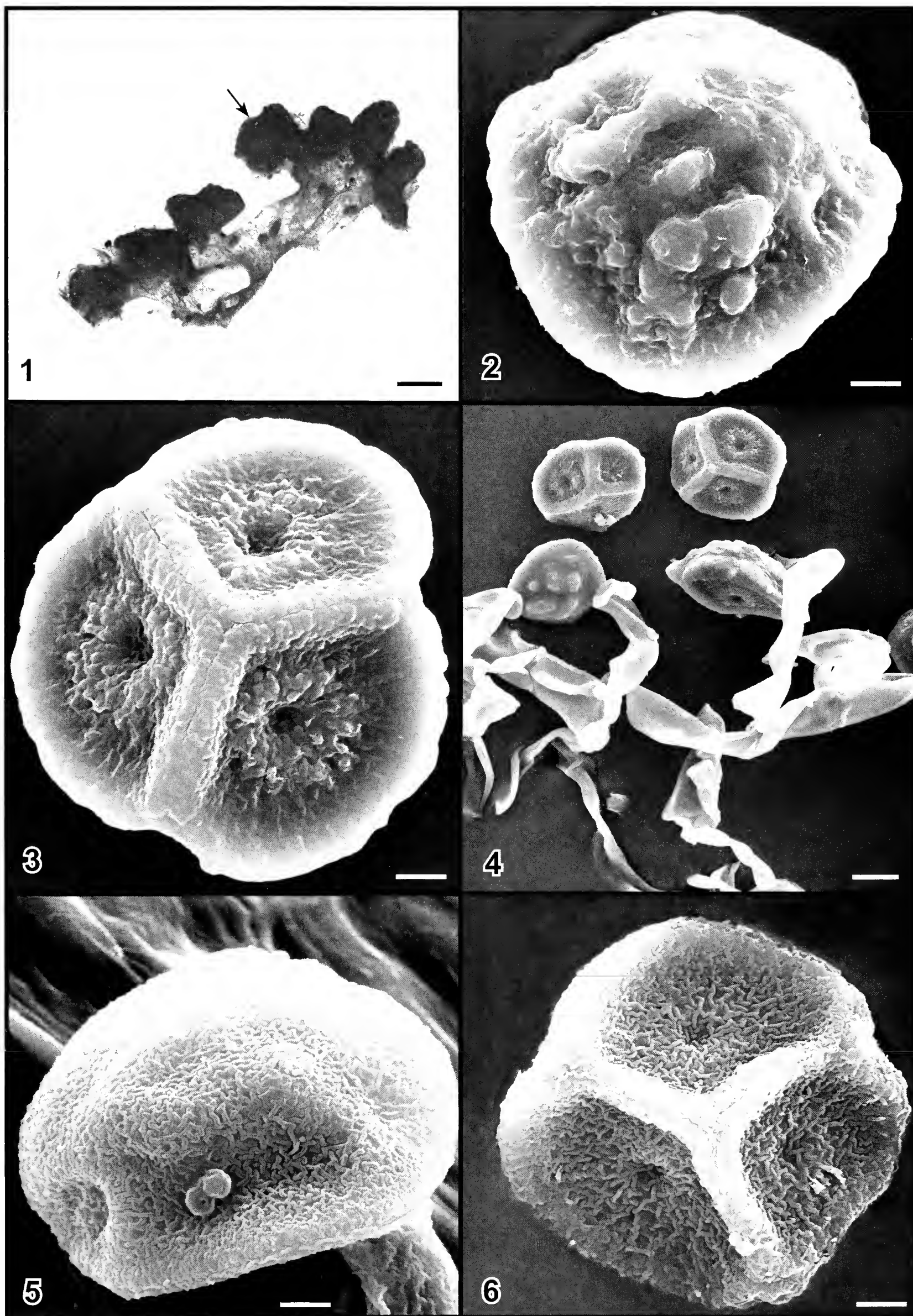


FIG. 5. *Paraphymatoceros diadenatus* Hässel (1–4) and *Paraphymatoceros coriaceus* (Steph.) Stotler (5, 6). 1. Tuber-bearing thallus, ventral view; at the arrow note the small rim of marginal cells extending beyond the tuber (1-mm scale). 2, 3. SEM of distal (2) and proximal (3) faces of mature spores from a dehiscent capsule (6- μ m scale in 2, 5- μ m scale in 3). 4. SEM of mature spores and pseudoelaters from a dehiscent capsule (20- μ m scale). 5, 6. SEM of distal (5) and proximal (6) faces of mature spores (5- μ m scale). [1–4 from the holotype; 5, 6 from *von Konrat s.n.*]

lines, and the valves are helically twisted and apically free. The capsule wall is 5 to 7 cell layers thick, consisting of an epidermis with thickened, pigmented outer tangential and radial walls, 3 to 5 layers of plastid-containing assimilatory cells, and an inner “endodermis” with thickened radial and inner tangential walls. Cells of both the epidermis and “endodermis” are rectangular in transverse section, whereas the assimilatory cells are isodiametric to quadrate. Stomates are widely scattered throughout the epidermis. The columella consists of 16 columns of thick-walled cells and protrudes as a rigid brown strand in dehiscing capsules.

Spores are mostly yellow to tawny but can be medium blackish brown near the capsule tip, and 40–50 μm in equatorial diameter. The distal surface is roughened with small papillae that gradate to short vermiculate thickenings and 2 to 12 large rounded protuberances or ridges, 5–6 μm in both height and diameter (Fig. 5.2). The proximal face is roughened with coarse, vermiculate thickenings and bears a prominent trilete ridge; each facet bears a central depression that averages 5.0 μm in diameter (Fig. 5.3). A ring of somewhat higher, coarser thickenings radiate out from the depressions, gradating into the finer vermiculate strands near the edges of the facet. Hässel de Menéndez (2006) describes the proximal facets as having “a crown of baculae surrounding a depressed area,” but in SEM micrographs, the “crown” appears to be made up of coarser, fused extensions of the vermiculate background, not rod-shaped baculae. Pseudoelaters are blackish brown, frequently branched, 3 or 4 cells long in the median part of the capsule, with individual cells 9.0–10.0 μm wide and 80–100 μm long. They typically fragment into shorter, 1- or 2-celled structures in the zone of dehiscence.

Hässel de Menéndez (2006: 210) included *P. hallii* in *Paraphymatoceros*, noting that it produces tubers and referencing an illustration of spores from Hässel de Menéndez, 1989: fig. 13. However, the spore proximal face in *P. diadematus*, which is the type species of the genus, is very different from that of *P. hallii*, as well as *P. pearsonii* and *P. proskaueri* (compare Figs. 5 and 6). There is, in fact, more resemblance to the proximal face architecture found in some species of *Phaeomegaceros* (Fig. 5.5, 5.6). For example, in *Phaeomegaceros coriaceus* (Steph.) Duff et al., each facet of the proximal face is covered with vermiculate thickenings and bears a central depression that is ringed by radiating thickenings;

in contrast to *Paraphymatoceros*, however, the distal spore face is also densely vermiculate and is marked with a few shallow depressions and 2 to 4 protuberant ridges (see also Campbell, 1982: fig. 4). Spores with proximal face depressions, or fovea, also occur in *Phaeoceros foveatus* J. Haseg., a southeast Asian species that is closely related to *Phaeomegaceros fimbriatus* (Gottsche) Duff et al. (Hasegawa, 2001: Fig. 2; Villarreal & Renzaglia, 2006), as well as *Phaeoceros himalayensis* (Kash.) Prosk. (Asthana & Srivastava, 1991: pl. 48) and *Notothylas dissecta* Steph. (Hässel de Menéndez, 1976: fig. 1). Furthermore, in the latter two species, the spores are initially yellow but become brown before natural dehiscence (Proskauer, 1967; Hässel de Menéndez, 1976).

In addition to producing foveate spores with an underlying matrix of vermiculate thickenings, other characters supporting the relationship between *Paraphymatoceros* and *Phaeomegaceros* include the following: the absence of a pyrenoid in the chloroplasts, rhizoids with flared tips, a dioicous sexual condition, a capsule wall with epidermal stomates and 5 or more layers of assimilatory cells, branched pseudoelaters, and two apically free, helically twisted capsule valves. According to Duff et al. (2007), all species of *Phaeomegaceros* are monandrous, but Campbell and Hasegawa (1993) report 4 antheridia per cavity in *Phaeomegaceros hirticalyx* (Steph.) Duff et al., as is also the case in *Paraphymatoceros* (Hässel de Menéndez, 2006). Morphological evidence suggests that *P. diadematus* is remote from the *P. hallii* group and supports its placement with the currently recognized species of *Phaeomegaceros*.

Molecular Evidence and Phylogeny

In both maximum parsimony (MP) and maximum likelihood (ML) analyses of *rbcL* sequence data, *P. proskaueri*, *P. hallii*, and *P. pearsonii* form a well-supported lineage, designated as the *P. pearsonii* clade, within a *Phaeoceros* + *Notothylas* clade (Fig. 7), with BS values of 99% (MP) and 96% (ML). Within the *P. pearsonii* clade, *P. proskaueri* is resolved as sister to *P. hallii*, with *P. pearsonii* sister to the *P. proskaueri* + *P. hallii* clade. The relationship of the *P. pearsonii* clade to the *Notothylas* clade or the *Phaeoceros carolinianus* (Michx.) Prosk. + *P. laevis* clade is unresolved in MP. In ML, the *Notothylas* clade is

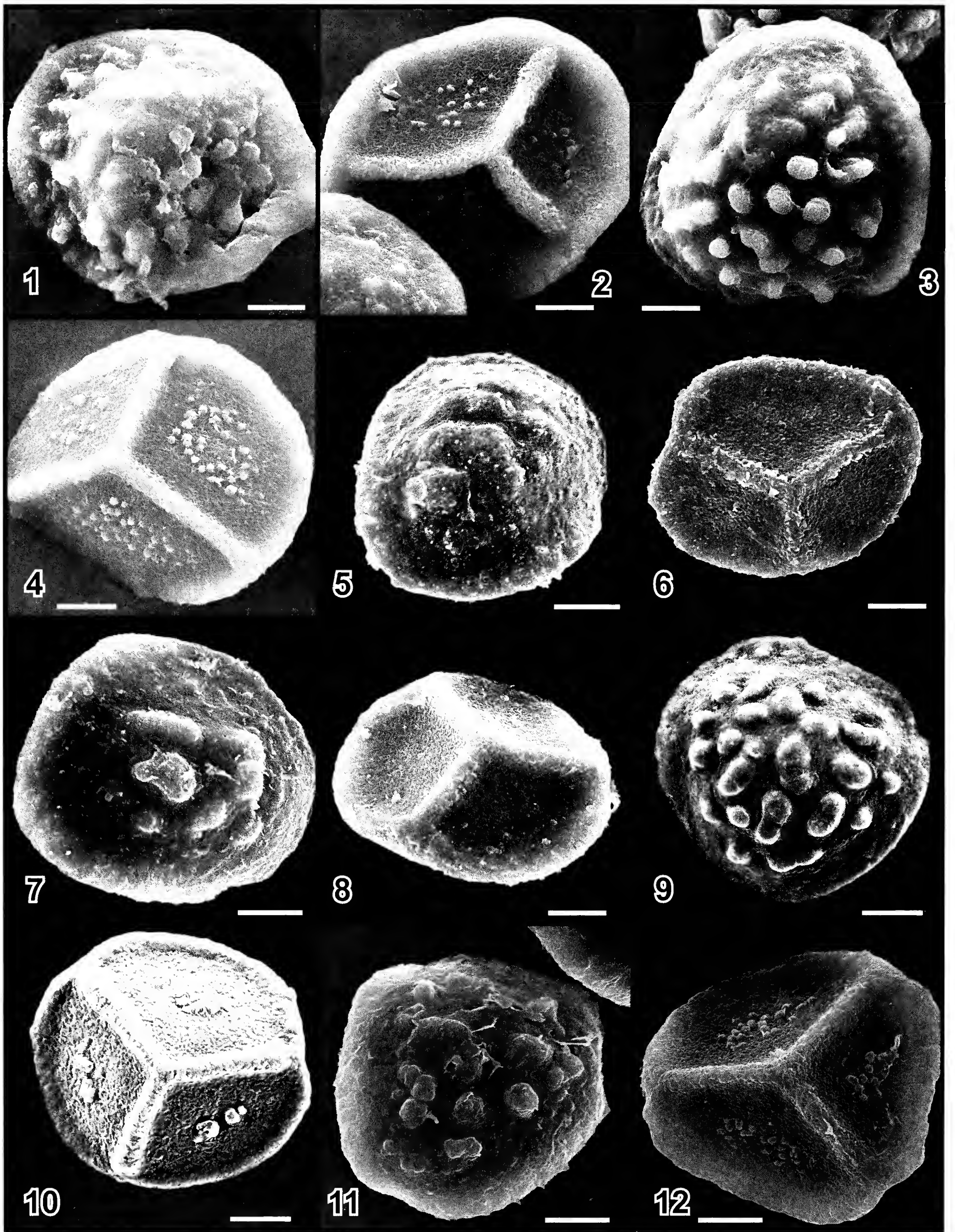


FIG. 6. SEM images of spore wall architecture in type specimens of the *Phaeoceros hallii* species complex (1–10) and spore variation in *Phaeoceros pearsonii* (M. Howe) Prosk. (11–12). 1, 2. Lectotype of *Anthoceros hallii* Austin [MANCH]. 3, 4. Lectotype of *Anthoceros sulcatus* Austin [MANCH]. 5, 6. Isotype of *Anthoceros pearsonii* M. Howe [UC]. 7, 8. Isotype of *Anthoceros bolanderi* Steph. [UC]. 9, 10. Holotype of *Phaeoceros proskaueri* Stotler, Crand.-Stotl. & W. T. Doyle [UC]. 11, 12. Atypical spores that are blackish brown and have several proximal facet papillae (from Wagner m1387) (all scales are 10 μ m).

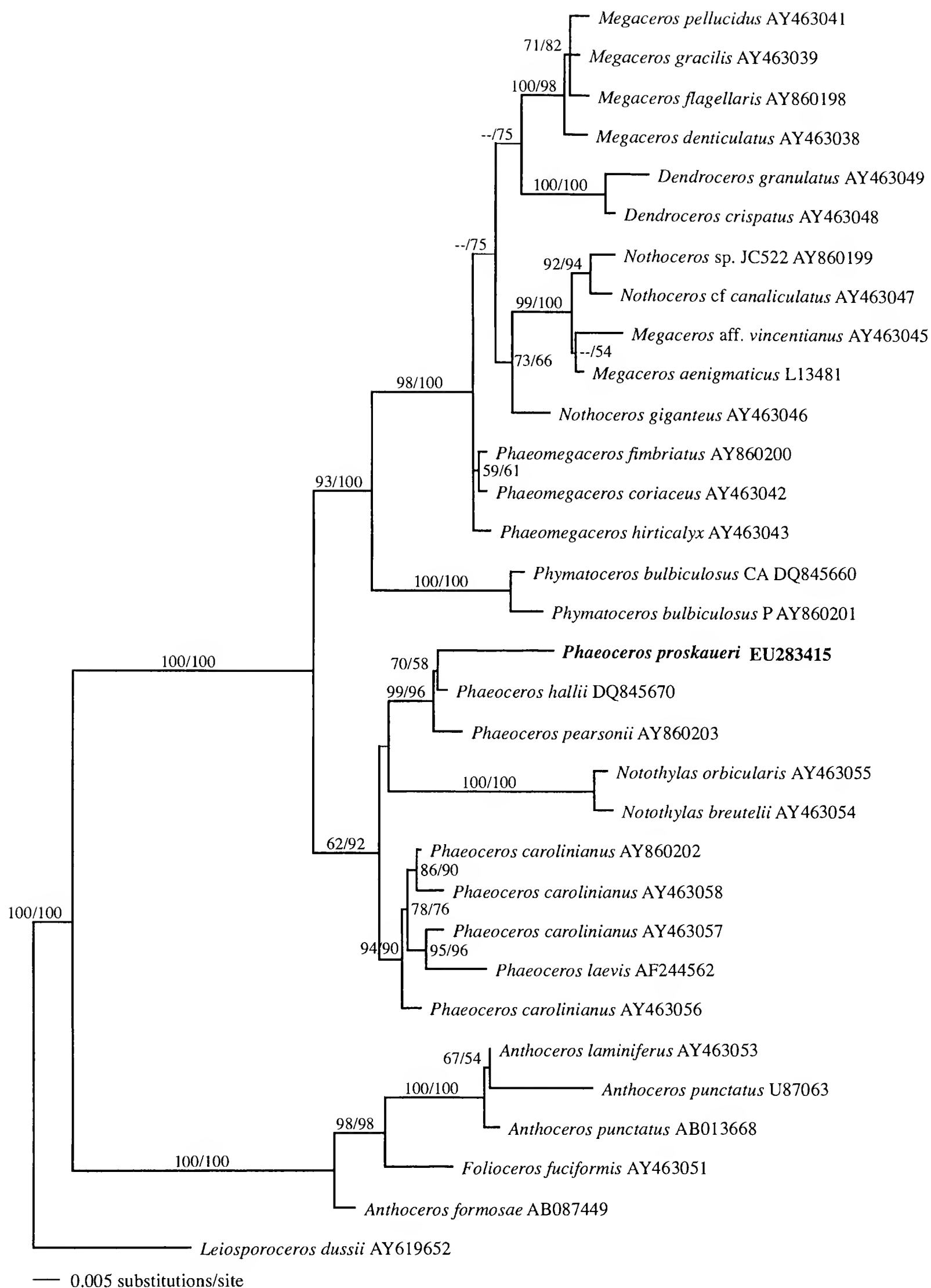


FIG. 7. Likelihood phylogram for hornworts based on chloroplast *rbcL* sequence data, generated using the general time reversible model. The first number above or to the right of branches is the MP bootstrap value and the second represents likelihood bootstrap support. Slender branches were not recovered by parsimony analyses.

recovered as sister to the *P. pearsonii* clade, but with less than 50% BS support. These results are congruent with the MP and Bayesian reconstructions of Duff et al. (2007).

As can be seen from the branch length on the phylogram (Fig. 7), the level of genetic divergence

between *P. proskaueri* and *P. hallii* supports the recognition of *P. proskaueri* as a distinct species of the *P. pearsonii* clade, as predicted by our morphological studies. The defining characters of the clade include perennation through apical or marginal tubers; thalli more or less strap-shaped

and not forming rosettes; capsule dehiscence along a single longitudinal slit, usually without helical twisting of the wall; spores yellow when immature, sometimes becoming darkened with secondary deposits late in development; spore walls with a vermiculate network of thickenings, overlaid distally by rounded protuberances or ridges and proximally often with a central group of papillae. *Phaeoceros hallii* has plastids with a distinct pyrenoid-like central region and 2–4 antheridia in each antheridial cavity, whereas *P. proskaueri* and *P. pearsonii* lack pyrenoids in their plastids and are monandrous. Obviously, neither the lack of a pyrenoid nor monandry are necessarily lineage-defining characters, being expressed in representatives of numerous lineages, including *Phymatoceros* (Crandall-Stotler et al., 2006), *Paraphymatoceros* (Hässel de Menéndez, 2006), *Phaeomegaceros* (Villarreal & Renzaglia, 2006), and other elements of the subclass Dendrocerotidae Duff et al. (Duff et al., 2007).

Morphological data support the notion of a relationship between the *P. pearsonii* clade and some species of *Notothylas*, as first discussed by Austin (1875). The capsules of *P. hallii* resemble those of *Notothylas* in being short, synchronous in sporogenesis and often indehiscent, but differ in having stomates in the capsule wall and an erect rather than horizontal orientation. Spore wall architecture in *N. orbicularis* is very similar to that of *P. pearsonii* (Schuster, 1992: fig. 1055) and the spores of *N. breutelii* (Gottsche) Gottsche become fuscous at maturity. Worldwide, *Notothylas* is morphologically heterogeneous and it is likely that with further sampling, the genus will be resolved as paraphyletic. Nonetheless, the clade containing *N. orbicularis* is either nested in or sister to the genus *Phaeoceros* (Duff et al., 2007), and the affinities of the *P. pearsonii* clade are with it and the genus *Phaeoceros*.

Taxonomy

NOTOTHYLADACEAE (Milde) Prosk., *Phytomorphology* 10: 10. 1960.

PHAEOCEROTOIDEAE Hässel, J. Hattori Bot. Lab. 64: 81. 1988.

PHAEOCEROS Prosk., Bull. Torrey Bot. Cl. 78: 346. 1951.

Phaeoceros hallii (Austin) Prosk., Bull. Torrey Bot. Club 78: 347. 1951.

Anthoceros hallii Austin, Bull. Torrey Bot. Club 6: 26. 1875. Lectotype (designated by M. Howe, Bull. Torrey Bot. Club 25: 11. 1898): USA, Oregon [Marion County], 26, Springy Places, Silverton, *Hall* [26] (MANCH—EM74235/21217!; isoelectotypes MANCH (2!) EM74234/21216, EM74241/21224; Paratype: USA, Oregon [Marion County], Dripping rocks, Salem, *Hall* [35] (MANCH (2!) EM74232/21214, EM74237/21219).

Anthoceros sulcatus Austin, Bull. Torrey Bot. Club 6: 27. 1875. Lectotype, designated here: USA, Oregon [Marion County], 25, moist earth, Salem, Oregon, *Hall* [25] (MANCH—EM74240/21223!; isoelectotypes MANCH (4!) EM74233/21215, EM74236/21218, EM154642/21221, EM74239/21222).

Notothylas hallii Austin ms., Bull. Torrey Bot. Club 6: 27. 1875.

Paraphymatoceros hallii (Austin) Hässel, *Phytologia* 88: 209. 2006. syn. nov.

Phaeoceros pearsonii (M. Howe) Prosk., Bull. Torrey Bot. Club 78: 347. 1951.

Anthoceros pearsonii M. Howe, Bull. Torrey Bot. Club 25: 8 + pl. 322–323. 1898. “*pearsoni*.” Holotype: USA, California, Marin County, Mill Valley, 7 May 1892, Howe 16 (NY—non vidi); isotype: (UC!).

Anthoceros bolanderi Steph., Sp. Hepat. 5: 975. 1916. Lectotype (designated by G. Hässel de Menéndez, *Candollea* 44: 731. 1989): USA, California, Mendocino City, *Bolander* (ex Herb. Gottsche) (G—non vidi; isotype: UC!).

Phaeoceros proskaueri Stotler, Crand.-Stotl. & W. T. Doyle, sp. nov.

Plantae thalloides, dioicae, dimorphae; thallus parvus, crassus, angustus, linearis, ramosus irregulariter, tuberculis numerosis subsphaeroides in ramis brevissimis lateralibus; cellulae chloroplasto uno; chloroplasti sine pyrenoidibus; androecium monandrum; capsula stomatophora, columella brunnea, rigida; sporae brunneae vel fuscae ubi maturis; pseudoelateres pallidi-brunnei, 2- vel 3-cellularis.

Plants prostrate, gregarious, forming mats; thallus segments linear, irregularly branched, with the branches subparallel to somewhat spreading and linear-oblong to narrowly lingulate, with a broad, thick central midrib that bears rhizoids ventrally, with the margins irregular and slightly upturned, constricted to 2 cells; plastids 1 per

cell, spheroidal to spindle-shaped, lacking a pyrenoid; rhizoids hyaline, abundant, mostly granulate, nongranulate (smooth) near the apex or on developing tubers, never adherent or fascicled; tubers abundant, at the apices of very short lateral branches, pale green, becoming brown at maturity, subspheroidal, less than 1 mm in diameter, on female plants rarely strongly flattened; plants dioicous, dimorphic; male thalli 0.3–0.8 mm wide; antheridial chambers near the base of the male thalli, with 1 antheridium per chamber; female thalli with sporophytes 1.5–2.0 mm wide; involucre short, 0.6–1.5 mm, narrowly campanulate, with the mouth flared; capsules 0.7–1.75 cm long (usually less than 1 cm), with the columella persistent, dehiscing by a single longitudinal slit along a suture line of yellow to orange cells; spores yellow to tawny when immature, becoming deep brown to fuscous when mature, 36–49 μm in diameter; spore proximal face trilete, with a small central cluster of 4 to 10 papillae on each facet; spore distal face with 13–30 rounded mammillae or elongate, rounded ridges, with a cingulum or wing; pseudoelaters brown, 2 or 3 cells long, fragmenting into 1(2)-celled structures near the capsule apex, each cell 12–18 μm wide, up to 40 μm long.

HOLOTYPE: CALIFORNIA; Monterey County. Fort Ord Public Lands–Bureau of Land Management, Barloy Canyon Road, nr Native Plant Reserve and Ft. Ord sign, hills primarily with coastal scrub chaparral, on north-facing slope on silty soil of roadcut, N 36°37'99", W 121°44'14", ca. 133 m.s.m., 14 April 2005, *Doyle 11350* (UC; Isotypes: ABSH, BA, BM, FH, G, MANCH, NY, W).

This species is named to honor Dr. Johannes Max Proskauer, who was the world's leading authority on hornworts at the time of his death in 1970. We are pleased that the species to bear his name is an element of *Phaeoceros*, a genus that he erected as a consequence of his doctoral research on the morphology of *Anthoceros* (Proskauer 1951).

Phaeoceros tuberosus (Taylor) Prosk., J. Indian Bot. Soc. 42A: 185. 1964.

Anthoceros tuberosus Taylor, Lond. J. Bot. 5: 412. 1846. Lectotype, designated here: Australia, “*Anthoceros tuberosus* MSS. T[homas]. T[aylor]., Swan River. Mr. James Drummond 1843” (FH!). [Although Proskauer annotated this specimen as the “Lectotype” he never published that choice.]

DENDROCEROTACEAE (Milde) Hässel, J. Hattori Bot. Lab. 64: 82. 1988.

PHAEOMEGACEROTOIDEAE Duff, J. Villarreal, Cargill & Renzaglia, Bryologist 110: 241. 2007.

PARAPHYMATOCEROS Hässel, Phytologia 88: 208. 2006. [*PHAEOMEGACEROS* Duff, J. Villarreal, Cargill & Renzaglia, Bryologist 110: 241. 2007. syn. nov.]

Paraphymatoceros diadematus Hässel, Phytologia 88: 209. 2006. (Holotype: CHILE, R V [Región de Valparaíso], Cachagua, Qda. Aguas Claras, En paredón húmedo junto al sendero, 05-Nov-05, Col. C. Villagrán 1115, Det. Hässel de Menéndez 2006, Holotipo (SGO: 153453!); paratypes: R V, Cachagua, Qda. Aguas Claras En paredón húmedo junto al sendero, 18-Sep-05, Col. C. Villagrán 1029, Det. Hässel de Menéndez 2006, Topotipo (SGO: 153454!); R V, El Tabo, Quebrada de Córdoba, Ladera de exposición sur. Matorral esclerófilo, 21-Ago-06, Col. C. Villagrán 1038, Det. Hässel de Menéndez 2006, (SGO: 153455!). [Hässel de Menéndez (2006) cited Villagrán 1029 and 1038 from Córdoba; this is correct for 1038, but 1029 is from the type locality of Qda. Aguas Claras.]

Hässel de Menéndez (2006) intended to include three species in her genus *Paraphymatoceros*, but she inadvertently transferred *Anthoceros minutus* Mitt., an African species, to the genus *Phymatoceros* Stotler, Crand.-Stotl. & Doyle, not *Paraphymatoceros*. We have not studied that taxon, but her inclusion of *Phaeoceros hallii* in *Paraphymatoceros* is shown here to be misplaced, in that it clearly belongs with *P. pearsonii* and *P. proskaueri*. Although Hässel de Menéndez (2006) placed her new genus into Notothyladaceae subfamily Phaeocerotoideae, our study of *P. diadematus* revealed that it is not only more appropriately aligned with *Phaeomegaceros* but can be regarded as congeneric with that taxon. Because *Paraphymatoceros* has priority, the following new combinations are made.

Paraphymatoceros fimbriatus (Gottsche) Stotler, **comb. nov.** Basionym: *Anthoceros fimbriatus* Gottsche, Ann. Sci. Nat. Bot. sér. 5. 1: 187–188. 1864.

Paraphymatoceros coriaceus (Steph.) Stotler, **comb. nov.** Basionym: *Anthoceros coriaceus* Steph., Sp. Hepat. 5: 991. 1916.

Paraphymatoceros hirticalyx (Steph.) Stotler, **comb. nov.** Basionym: *Aspiromitus hirticalyx* Steph., Sp. Hepat. 5: 966–967. 1916.

Paraphymatoceros skottsbergii (Steph.) Stotler, **comb. nov.** Basionym: *Anthoceros skottsbergii* Steph., Kongl. Svenska Vetenskapsakad. Handl. 46: 90. 1911.

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Appendix

ADDITIONAL SPECIMENS EXAMINED—*Paraphymatoceros coriaceus*. NEW ZEALAND. s.l., (rec'd. 23 March 2006 acc. BJCS 583), *von Konrat s.n.* (ABSH). *Paraphymatoceros diadematus*. CHILE. R V [Región de Valparaíso], Zapallar, Quebrada El Tigre. Naciente de la quebrada, al llegar al Alto del Bolfo. 26-Ago-06, Col. C. Villagrán 1017, Det. Hässel de Menéndez 2006, (SGO: 153456). *Phaeoceros hallii*. USA California—EL DORADO COUNTY: Sierra Nevada foothill, Sand Ridge Road ca. 4.7 mi W of jct. with Buck's Bar Road, soil of hillside, elev. ca. 1200 feet, 26 April 1996, *Doyle 8258* (ABSH, UC); Sierra Nevada western slope, Sand Ridge Road at hairpin turn, ca. 1 mi E of jct. with CA Hwy 49, seepage at base of small sloping meadow, with scattered *Quercus* and *Pinus*, metamorphic substrate, shaded by grasses and *Mimulus*, ca. 365 m, N 38°35'78", W 120°49'98", 16 May 2005, *Doyle 11363*, 25 May 2005, *Doyle 11366* (ABSH, UC); MADERA COUNTY: Sierra Nevada foothill, along CR 274 E of Bass Lake, on thin soil, seepage over granite slab in a small meadow, elev. ca. 3450 feet, 30 April 1996, *Doyle 8276* (ABSH, UC); Sierra Nevada, Oak Grove Road, ca. 4.4 mi W of Madera/Mariposa County line, nr oaks, bases of roadcut, in grass, elev. ca. 700 feet, 9 April 1996, *Doyle 8193*, 30 April 1996, *Doyle 8272*, 20 May 1996, *Doyle 8445* (ABSH); Sierra Nevada, Oak Grove Road ca. 2.3 mi W of

Madera/Mariposa County line, soil of roadcut, elev. ca. 800 feet, 30 April 1996, *Doyle 8271* (ABSH); Sierra Nevada, E side of Auberry Road ca. 1.5 mi N of bridge across San Joaquin River, shade of oaks, seepage, depression in hillside, elev. ca. 2400 feet, 30 April 1996, *Doyle 8292* (ABSH); Sierra Nevada, W side of CR 415 ca. 7.2 mi N of Coarsegold on SR 41, scattered oaks, under grass of "mouse runs" nr hillside seepage, elev. ca. 2000 feet, 20 May 1996, *Doyle 8446* (ABSH); MARIPOSA COUNTY: Sierra Nevada foothills, along Oak Grove Road ca. 3.9 mi E of Mariposa/Madera County line, seepage over granite, elev. ca. 1000 feet, 30 April 1996, *Doyle 8269* (ABSH, UC); Sierra Nevada, Oak Grove Road ca. 1.7 mi E of Mariposa/Madera County line, soil of hillside, elev. ca. 900 feet, 30 April 1996, *Doyle 8270* (ABSH); MODOC COUNTY: Modoc National Forest, Yellow Jacket Springs Road ca. 0.8 mi W off National Forest Service Road 84, W off CA 299 nr Canby Bridge, bank of ephemeral creek, shade of pines, 19 July 1995, *Doyle 7486* (ABSH); Modoc National Forest, Yellow Jacket Springs ca. 0.8 mi W off National Forest Service Road 84, volcanic substrate, elev. ca. 4500 feet, 3 August 1996, *Doyle 8649* (ABSH, UC); Modoc National Forest, Yellow Jacket Springs Road, W off National Forest Service Road 84, N off CA 299 nr Canby Bridge, volcanic substrate, on soil bank and rock in bed of ephemeral creek in a pine forest, elev. ca. 1365 m, 26 July 2005, *Doyle 11390* (ABSH, UC); NEVADA COUNTY: Sierra Nevada, Garden Bar Road ca. 2.1 mi SW of jct. with Wolf Road, soil of roadbank, elev. ca. 800 feet, 27 April 1996, *Doyle 8319* (ABSH, UC); TRINITY COUNTY: Klamath Range, NE side of Trinity Lake, Eastside Road ca. 4.8 mi E of jct. with SR 3, drainage through meadow in oak woodland, elev. ca. 3000 feet, 12 June 1996, *Doyle 8545* (ABSH, UC). *Phaeoceros pearsonii*. USA CALIFORNIA—ALAMEDA COUNTY: Diablo Range, Calaveras Road, S off Interstate Hwy 680, Sunol Regional Wilderness, hillside seepage on N side of creek, ca. 228 m.s.m., 18 May 1983, *Doyle 3139* (UC); AMADOR COUNTY: Western foothills of Sierra Nevada, Clinton Road, ca. 0.8 mi E of jct. with CA Hwy 49, nr Jackson, mixed *Quercus* and *Arbutus*, soil of hillside on S side of road, ca. 380 m.s.m., 21 May 1996, *Doyle 8449* (UC); BUTTE COUNTY: Sierra Nevada, NE of Oroville, North Table Mountain, scattered *Quercus*, volcanic plateau, on soil of shaded drainage, elev. ca. 363 m, 4 May 1999, *Doyle 9706* (UC); CALAVERAS COUNTY: Western foothills of Sierra Nevada, NE

of Altaville, Gogtown Road ca. 0.3 mi W of jct. with Esmeralda Road, soil of hillside, with grass under *Quercus*, 26 April 1996, *Doyle 8248* (UC); CONTRA COSTA COUNTY: Central Coast Region, Morgan Territory Road, ca. 7.9 mi N of jct. with North Livermore Road, mixed *Quercus*, *Lithocarpus*, and *Umbellularia*, soil of roadcut, elev. ca. 150 m, 11 April, *Doyle 8938* (UC); EL DORADO COUNTY: western slope of Sierra Nevada, Sandridge Road, nr 3.76-mi marker, E off CA 49, nr scattered *Quercus* and *Arbutus*, on soil on exposed vertical slope of hillside nr creek, elev. ca. 575 m, 28 May 1996, *Doyle 8463* (UC); HUMBOLDT COUNTY: North Coast Ranges, CA Hwy 36 nr 36.39 mi marker, small creek and road cut on S side of road, mixed *Lithocarpus*, *Pseudotsuga*, *Umbellularia*, and *Acer*, shaded, slow-drying soil of creek bank and road cut, N 40°27'07", W 123°39'09", ca. 810 m.s.m., 1 June 2005, *Doyle 11386* (UC); MARIN COUNTY: North Coast Region, Bolinas–Fairfax Road nr Alpine Dam, nr *Sequoia* and *Quercus*, on soil nr base of road cut, ca. 150 m.s.m., 14 May 1996, *Doyle 8423* (UC); North Coast Region, Sir Francis Drake Boulevard, Samuel P. Taylor State Park, *Sequoia*, *Lithocarpus*, *Acer*, and *Alnus*, soil on shaded bank of Lagunitas (Papermill) Creek, elev. ca. 45 m, 3 June 2003, *Doyle 10536* (UC); MENDOCINO COUNTY: North Coast Region, rest area on W side of US 101, nr 101 MEN 58.6 mi marker, canyon W of rest area, mixed *Lithocarpus*, *Quercus*, *Acer*, and *Pseudotsuga*, on soil, steep side of canyon above creek, elev. ca. 350 m, 14 September 1995, *Doyle 7776* (UC); North Coast Region, CA Hwy 1, ca. 1.1 mi W of Leggett, *Sequoia* forest, on soil of road cut, elev. ca. 335 m, 30 April 1997, *Doyle 8974* (UC); North Coast Ranges, Low Gap Road ca. 7.4 miles W of Ukiah, oak, Douglas fir, maple, blackberry, and poison oak, soil of shaded, north-facing roadside drainage, N 39°09'58", W 123°19'86", ca. 730 m.s.m., 31 May 2005, *Doyle 11377* (UC); North Coast Ranges, Low Gap Road, ca. 5.2 mi W of Ukiah, mixed *Lithocarpus*, *Pseudotsuga*, and *Acer*, small creek and spring on S side of road, shaded, slow-drying soil, N 39°09'58", W 123°19'86", ca. 760 m.s.m., 31 May 2005, *Doyle 11378* (UC); MONTEREY COUNTY: Santa Lucia Range, Los Padres Natl. Forest, Ventana Wilderness, Pine Ridge Trail, Trailhead at Big Sur Station on CA Hwy 1, *Sequoia*, *Acer*, *Lithocarpus*, and *Alnus*, on soil of hillside along trail, R2E T19S S21, ca. 212 m.s.m., 11 May 1994, *Doyle 6418* (UC); PLACER COUNTY: Sierra Nevada, SW of Applegate, Clipper Gap Road, ca. 0.25 mi

S of jct. with Pepper Ranch Road, scattered oaks on hillside, shaded drainage along road, on soil, elev. ca. 576 m, 19 May 2002, *Doyle 9963* (UC); North Fork of the Middle Fork of American River at Mosquito Ridge Road, shaded roadbank in *Pinus ponderosa*–*Quercus chrysolepis*–*Pseudotsuga* forest, N 39°01.5', W 120°43', elev. 1300 feet, 2 May 1992, *A.T.&T. E. Whittemore 3985* (ABSH); SAN BENITO COUNTY: Central Coast Region, Diablo Range, NE of Hollister, Lone Tree Road, ca. 8.3 mi E of jct. with Fairview Road, creek bank on N side of Road, on soil, 10 May 1995, *Doyle 7391* (UC); Gabilan Range, Pinnacles Natl. Monument, Moses Spring Trail, between trail markers 8 and 9, shade of toyon and oak, damp hillside along trail, N 36°28'53", W 121°11'21", ca. 500 m.s.m., 28 March 2005, *Doyle 11325*, 18 September 2005, *Doyle 11415*, 27 December 2005 *Doyle 11420*, 9 January 2006, *Doyle 11424*, 20 January 2006, *Doyle 11429* (UC); SAN LUIS OBISPO COUNTY: Santa Lucia Range, Santa Rita Road between Templeton and Cayucus, E side of summit, *Quercus*, *Pinus*, and chaparral, soil of shaded road cut, ca. 273 m.s.m., 19 April 1993, *Doyle 5726* (UC); North Coast Ranges, Montana de Oro State Park, Coon Creek Trail, shade of *Salix*, *Quercus*, and *Umbellularia*, on soil of creek bank, R10E T31S, elev. ca. 45 m, 28 April 1998, *Doyle 9481* (UC); Santa Lucia Range, Santa Rita Road ca. 1.7 miles E of jct. with Old Creek Road, mixed *Quercus*, *Lithocarpus*, *Acer*, *Umbellularia*, and *Salix*, damp, slow-to-dry soil of road cut under *Adiantum*, N 35°28'65", W 129°50'10", ca. 120 m.s.m., 12 April 2005, *Doyle 11346* (UC); SAN MATEO COUNTY: Central Coast Region, Santa Cruz Mountains, San Pedro Valley County Park, Hazelnut Trail, sedimentary substrate, scattered chaparral and *Quercus*, on soil, hillside along trail, R6W T4S S24, elev. ca. 105 m, 1 May 2003, *Doyle 10380* (UC); SANTA BARBARA COUNTY: South Coast Region, Transverse Ranges, Santa Ynez Mountains, S side of road between US Hwy 101 and Nojoqui Falls County Park, oaks and shrubs, shaded soil of hillside, R31W T5N S12, 6 April 1995, *Doyle 7174* (UC); South Coast Region, Purisima Hills, La Purisima Mission State Historic Park, shade of *Salix*, on soil, bank of Purisima Creek, elev. ca. 105 m., 27 April 1998, *Doyle 9473* (UC); SANTA CRUZ COUNTY: Central Coast Region, Santa Cruz Mountains, Branciforte Drive, just E of Goss Avenue, shaded, base of vertical sandstone outcrop on S side of road, on spoil, elev. ca. 42 m, R1W T11S S7, 9 May 1994, *Doyle 6380* (UC);

Central Coast Region, Santa Cruz Mountains, Fall Creek Unit of Henry Cowell Redwoods State Park, *Sequoia*, *Lithocarpus*, *Acer*, and *Umbellularia*, North Fork Trail, nr jct. with South Fork Trail, on soil of N facing cliff face along trail, elev. ca. 180 m, R2W T10S S16, 3 May 1997, *Doyle 8941* (UC); Central Coast Region, Santa Cruz Mountains, Mt. Madonna County Park, CA Hwy 152, nr the 0.87 mi marker, nr small creek on N side of road, *Sequoia*, *Pseudotsuga*, *Lithocarpus*, and *Umbellularia*, on soil, seepage on an old logging road, elev. ca. 303 m, 19 May 2003, *Doyle 10465* (UC); Santa Cruz Mts., Nisene Marks State Park, along trail between park entrance kiosk and Aptos Creek, on soil along trail in grass, ca. 25 m.s.m., 10 January 2006, *Doyle 11426*, 20 January 2006, *Doyle 11428* (UC); SHASTA COUNTY: Klamath Ranges, Trinity Mountains, along Placer Road, SW of Redding, open, drying creek on N side of road, on soil of creek bank with grass and moss, elev. ca. 210 m, 12 May 1997, *Doyle 9117* (UC); SISKIYOU COUNTY: Klamath Ranges, Klamath National Forest, Forest Road 37N24, off Callahan-Cecilville Road, S of South Fork Campground, on soil, seepage into a roadside drainage ditch, elev. ca. 820 m, R11W T37N S10, 9 June 1993, *Doyle 5934* (UC); SONOMA COUNTY: North Coast Ranges, Cazadero Hwy, ca. 1.1 mi NW of Cazadero, mixed *Pseudotsuga*, *Sequoia*, *Acer*, and *Umbellularia*, shaded soil of roadcut, S side of road, elev. ca. 182 m, 3 May 2004, *Doyle 10941* (UC); TRINITY COUNTY: Klamath Ranges, South Fork of Trinity River Road, ca. 3.8 mi S of jct. with CA Hwy 299, shaded soil of road cut, R5E T6N S25, ca. 242 m.s.m., 13 June 1996, *Doyle 8555* (UC); TULARE COUNTY: Sierra Nevada, Sequoia Natl. Forest, Kaweah River drainage, North Fork Road S from Three Rivers, on soil under shrubs at base of road cut, ca. 725 m.s.m., 6 May 1993, *Doyle 5807* (UC); YUBA COUNTY: Sierra Nevada, Tahoe National Forest, Handicap Trail of Independence-Yuba River Trail, off CA Hwy 49, NE of Nevada City, *Pseudotsuga*, *Quercus*, *Calocedrus*, *Pinus*, and *Lithocarpus* forest, on soil, shaded hillside along trail, elev. ca. 425 m, R8E T17N S33, 16 June 1998, *Doyle 9593* (UC); OREGON-LANE COUNTY: Trail along North Fork Middle Fork Willamette River, ca. 5 mi from Westfir Trailhead, ca. 30 mi SE of Eugene, on vertical soil bank that drips in the Spring, ca. 326.8 m.s.m., 19 July 2007, *Wagner m2269* (ABSH); LINN COUNTY, S. Santiam River, Hwy 20, Milepost 50, 29 June 2004, *Wagner m1387* (ABSH).

***Phaeoceros proskaueri*. USA CALIFORNIA-EL DORADO COUNTY:** Western foothills of Sierra Nevada, Rattlesnake Bar Road, ca. 1.6 mi W of jct. with CA Hwy 49 nr Pilot Hill, easily disturbed soil of hillside nr chaparral and oak, ca. 305 m.s.m., 28 May 1996, *Doyle 8466* (UC); Sandridge Road ca. 0.2 mi E of jct. with CA Hwy 49, open north-facing, easily disturbed soil of hillside, ca. 260 m.s.m., 28 May 1996, *Doyle 8454* (UC); Sandridge Road, ca. 7.8 miles W of jct. with Buck's Bar Road, easily disturbed soil of road cut, nr oak, ca. 305 m.s.m., 26 April 1996, *Doyle 8262* (UC); Western foothills of Sierra Nevada, Sandridge Road nr mile marker 3.67, soil, NW facing road cut, partial shade of *Umbellularia*, *Pinus*, and *Quercus*, N 38°35'95", W 120°47'50", ca. 440 m.s.m., 25 May 2005, *Doyle 11368* (ABSH, UC); MARIPOSA COUNTY: Sierra Nevada, western slope, Old Toll Road, ca. 0.65 mi W of CA Hwy 49 jct., chaparral-covered hillslope on N side of road, metamorphic substrate, on soil in shade of shrubs, on remnants of abandoned dirt road, ca. 600 m.s.m., N 37°30'58", W 120°03'41", 21 April 2005, *Doyle 11357* (ABSH, UC); Sierra Nevada western slope, W of Mt. Bullion, N side of Old Toll Road, ca. 0.65 mi. W of CA Hwy 49 jct., partial shade of chaparral, remnant of old dirt road, soil of roadbed, ca. 600 m.s.m., N 37°30'58.8", W 120°03'46", 10 January 2006, *Doyle 11425* (ABSH, UC); Western slope of Sierra Nevada, Old Toll Road, ca. 0.4 mi W of jct. with CA Hwy 49 at Mt. Bullion, S side of road, open areas in chaparral, easily disturbed soil of hillside, ca. 605 m.s.m., 30 April 1996, *Doyle 8267* (UC); MONTEREY COUNTY: Santa Lucia Range, nr gate to old Graniterock Quarry, 22 May 1995, *Doyle 7402* (ABSH); Fort Ord Public Lands, Bureau of Land Management, small canyon that crosses Crescent Bluff Road, ca. 0.3 mi S of junction with Barloy Canyon Road, open areas in chaparral and oaks, sandy soil, elev. ca. 225 ft., 10 April 2005, *Doyle 11339* (ABSH); Fort Ord Public Lands-Bureau of Land Management, Barloy Canyon Road, ca. 1.1 mi W of Crescent Bluff Road jct., nr Fort Ord sign, exposed NE facing slope, on fine-grained soil, N 36°37'99", W 121°44'14", ca. 125 m.s.m., 18 April 2005, *Doyle 11355* (ABSH, UC), 29 December 2006, *Doyle 11421* (ABSH), 5 January 2006, *Doyle 11422* (ABSH), 19 January 2006, *Doyle 11430* (ABSH); Fort Ord Public Lands-Bureau of Land Management, Crescent Bluff Road, ca. 0.5 mi south of jct. with Barloy Canyon Road, hillside with chaparral and scattered oak, soil, openings in chaparral, N 36°38'30", W 120°38'30",

ca. 95 m.s.m., 10 April 1996, *Doyle 8195* (UC); Fort Ord Public Lands—Bureau of Land Management, Eucalyptus Road, ca. 1.8 mi E of jct. with Parker Flat Road, oak woodland, soil of open areas on hillside, ca. 115 m.s.m., 15 April 1998, *Doyle 9453* (UC); Fort Ord Public Lands—Bureau of Land Management, Barloy Canyon Road, ca. 1.1 miles W of jct. with Crescent Bluff Road, chaparral covered hillside, soil of open, sloping drainage on N side of road, N36°38'1", W 121°44'16", ca. 125 m.s.m., 6 February 2006, *Doyle 11431* (ABSH, UC); Fort Ord Public Lands—Bureau of Land Management, Barloy Canyon Road, nr Native Plant Reserve and Ft. Ord sign, Hills primarily with coastal scrub chaparral, on north-facing slope on silty soil of roadcut, N 36°37'99", W 121°44'14", ca. 133 m.s.m., 24 February 2006, *Doyle 11433, 11434* (ABSH, UC); RIVERSIDE COUNTY: Peninsular Ranges, Santa Ana Mountains, Santa Rosa Plateau Ecological Reserve, soil of drainage on S side of Clinton Keith Road, with grass nr coastal sage scrub, ca. 545 m.s.m., 16 April 1995, *Doyle 7273* (UC); Peninsular Ranges, Santa Ana Mountains, Santa Rosa Plateau Ecological Reserve, Sylvan Meadow Ranch Unit, soil, open areas in coastal sage scrub, ca. 545 m.s.m., 25 April 1995, *Doyle 7268* (ABSH, UC); Peninsular Ranges, Santa Ana Mountains, Santa Rosa Plateau Ecological Reserve, W of old parking lot at main entrance to Reserve, soil, open grassy areas in coastal sage scrub, ca. 540 m.s.m., 26 April 1995, *Doyle 7275* (UC); Santa Ana Mts., Santa Rosa Plateau Ecol. Reserve, Sylvan Meadow Ranch Unit, N side of Clinton Keith Road, open areas nr and under coastal sage scrub, N33°32'40", W117°16'32", ca. 545 m.s.m., 4 May 2006, *Doyle 11450* (ABSH, UC); SAN DIEGO COUNTY: Forester Creek, nr jct. of La Cresta

Road and Old Bend road W of La Cresta, nr chaparral and oak, soil of open areas of hillside just above creek, ca. 240 m.s.m., 4 April 1995, *Doyle 7156* (UC); Kearney Mesa E off Eastgate Road, nr top of ravine overlooking Interstate Hwy 805, soil, open areas nr chaparral, R3W T15S S8, ca. 95 m.s.m., 3 April 1995, *Doyle 7194A* (UC); SAN LUIS OBISPO COUNTY: Eastern side of Santa Lucia Ranges, Chimney Rock Road W of Paso Robles, ca. 4.4 mi NE of jct. with Klaus Mine Road, soil, open areas on hillside with scattered oak, ca. 260 m.s.m., 23 April 1996, *Doyle 8210* (UC); SAN MATEO COUNTY: Eastern side of Santa Cruz Mts., Edgewood County Park, Sylvan Trail, soil nr top of trail bank at switchbacks, ca. 160 m.s.m., 7 April 1998, *Doyle 9442* (UC); SANTA BARBARA COUNTY: Transverse Ranges, Santa Ynez Mts., Los Padres National Forest, Snyder Trail S off Paradise Road, nr chaparral and oak, soil high on nr vertical bank of small ephemeral creek, ca. 335 m.s.m., 19 May 1998, *Doyle 9551* (UC); SANTA CLARA COUNTY: Diablo Range E of Gilroy, E side of Cañada Road, ca. 3.4 mi SW of jct. with Jamison Road, nr. oak and chaparral, ca. 115 m.s.m., 18 April 1978, *Doyle 2360* (UC); SANTA CRUZ COUNTY: Santa Cruz Mts., Santa Cruz campus of the University of California, Fuel Break Road nr jct. with Red Hill Road, chaparral and scattered oak, soil in openings of chaparral on hillside, ca. 290 m.s.m., 10 April 1997, *Doyle 8932* (UC); TUOLUMNE COUNTY: Western foothills of Sierra Nevada, Reynolds Ferry Road N of Tuttle Town, ca. 0.7 mi W of jct. with CA Hwy 49, ca. 260 m.s.m., 21 May 1996, *Doyle 8448* (UC); TULARE COUNTY: Sequoia National Park, on soil under weeds on a sloping hillside meadow (swale), 5 April 2005, *Doyle 11328* (ABSH, UC).

FIELDIANA

In celebration of Dr. John J. Engel: A tribute to 40 years in bryology

Botany

NEW SERIES, NO. 47

Part Eight: Hornworts

Chapter Twenty: Taxonomic Studies of the Australian Anthocerotophyta II: The Genus *Phaeoceros*

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Abstract

Four species within the hornwort genus *Phaeoceros* are recognized and described for Australia: the cosmopolitan *P. carolinianus* (Michx.) Prosk.; two new combinations of taxa endemic to Australia—*P. evanidus* (Steph.) Cargill & Fuhrer comb. nov., *P. inflatus* (Steph.) Cargill & Fuhrer comb. nov.; and a species new to science, *P. engelii* Cargill & Fuhrer sp. nov. A key to all four species is also given.

Introduction

The hornworts have become a pivotal group in understanding the transition from nonvascular land plants to vascular land plants (Qiu et al. 2006). A seemingly homogeneous group, recent molecular and ultrastructural studies have

revealed a surprisingly diverse group of plants. Traditional relationships have been discarded, such as that between *Anthoceros* L. emend. Prosk. and *Phaeoceros* Prosk., others have been confirmed, such as between *Megaceros* Campb. and *Dendroceros* Nees., and new and novel ones have been revealed, such as the position of the unique

Leiosporoceros Hässel (Duff et al., 2004, 2007; Cargill et al., 2005). These studies have concentrated on relationships at the level of genera and higher yet species boundaries within the group still remain confused. This paper is the second in a series revising the hornwort species of Australia and is a foundation paper for the genus *Phaeoceros* in this region.

Historical Review

After a comprehensive study of the hornworts, Proskauer (1951) circumscribed the genus *Phaeoceros* from the broadly defined *Anthoceros* on the basis mainly of the absence of internal schizogenous cavities in the thallus typically found in *Anthoceros*. However, characters considered of secondary importance included irregularly arranged antheridial jacket cells and yellow spores. Acceptance of the new genus was not universal and controversy surrounded its nomenclature until recently. The name *Anthoceros* has now been conserved for those elements that possess dark-colored spores and a cavernous thallus (Stotler & Crandall-Stotler, 2003).

After Proskauer's revisions for the genus *Phaeoceros*, a number of studies ensued. These included the studies of Hässel de Menéndez (1989) who recognized 23 species for North and South America. On the basis primarily of the patterns of the distal and proximal faces of the spores observed through scanning electron microscopy (SEM), she emphasized the importance of spore differences in the separation of species. She grouped the American species into four distinct categories on the basis of the patterns of the spore distal face: 1) spores with spines or baculae, for example, *P. carolinianus* (Michx.) Prosk. (Fig. 3.); 2) spores with large projecting verrucae, for example the spores of *P. tenuis* (Spruce) Hässel or *P. pearsonii* (M.A. Howe) Prosk. (Hässel de Menéndez, 1989); 3) spores with fine, low ornamentation, for example the spores of *Phymatoceros bulbiculosus* (Brot.) Stotler et al. (Crandall-Stotler et al., 2006); and 4) spores with depressions, for example the spores of *Phaeomegaceros fimbriatus* (Gottsche) Duff et al., (Hässel de Menéndez, 1989 as *Phaeoceros fimbriatus* Gottsche). These groupings were not given any taxonomic status by Hässel, but recent molecular studies have partially supported these categories, giving rise to three new genera, a new family, and a new subfamily: *Phymatoceros* Stotler, W.T. Doyle &

Crand.-Stotl. (category 2) (family Phymatocerotaceae Duff et al.); *Paraphymatoceros* Hässel (category 3); and *Phaeomegaceros* Duff et al. (category 4) (subfamily Phaeomegacerotoideae Duff et al.). Hässel's study highlighted the broad diversity of spore patterning within this group, and recent molecular results have confirmed the importance of spore characters as well as highlighting the importance of others such as chloroplast, pyrenoid, or tuber morphology.

History of Australian Taxa

The earliest record of an Australian hornwort was made by Lehmann and Lindenberg in 1832 describing *Anthoceros adscendens* and *A. glandulosus* (Lehmann 1832). Over the next 80 years, only 11 more taxa were added to the Australian records until the comprehensive publications of Stephani in 1917. He attributed 19 anthocerotes to Australia, of which eight were new to science and two species were new records for Australia. Of the 29 taxa recorded for Australia (many of which are yellow spored), only two species have been recognized for the genus *Phaeoceros*: *P. laevis* and *P. carolinianus* (McCarthy 2006). Scott and Bradshaw's important foundational checklist of Australian liverworts (Scott & Bradshaw 1985) did not accept the generic rank of *Phaeoceros*. Instead they preferred to follow Jones' (1958) and Schuster's (1963) placement as a subgenus of *Anthoceros*. Molecular studies have subsequently supported Proskauer's original split of *Anthoceros* into two distinct genera (Duff et al., 2004, 2007; Frey & Stech, 2005), and the genus *Phaeoceros* is universally accepted.

A number of regional revisions of *Phaeoceros* have been published over the last two decades, including Japan, South East Asia, and islands of the Pacific (Hasegawa, 1984a, b, 1986a, b, 1991, 1993, 2002), New Zealand (Campbell, 1981a, b, 1982, 1993), North and South America (Hässel de Menéndez, 1989; Schuster 1992), and India (Asthana & Srivastava, 1990). However, since the prodigious publication of Stephani (1900–1924), no comprehensive revision of the hornworts for Australia has been undertaken. The aim of this paper is to determine the status of the yellow-spored taxa previously published for Australia. Also included is the description of a new species, *P. engelii* named in celebration of John Engel's 40 years of publications in the field of bryological studies.

Materials and Methods

The type specimens of all yellow-spored taxa originally described for Australia were examined, including collections of *Phaeoceros* from all major Australian herbaria. Field collections were also made over a wide geographical range within Australia. Where mature sporophytes were present, spores were sampled for viewing with SEM. Air-dried spores were removed from capsules and mounted on double-sided sticky tape attached to aluminum stubs. Stubs were gold coated and viewed with either a Hitachi S-570 or a Jeol JSM 6400 SEM. Spores and pseudoelaters were also mounted in water for measurement and color information with subsequent permanent mounting in either Hoyer's or Johnson Brite®.

Both rehydrated herbarium specimens and live field collections were examined, sectioned, measured and drawn for gametophytic and sporophytic characters with the use of both compound and dissecting microscopes with attached drawing tubes. Habit and light microscope images of *Phaeoceros* were taken with a Nikon Coolpix 5000 digital camera.

Colors of gametophytes were determined by the use of the Royal Horticultural Society Colour Chart (1995).

Results

Type specimens of all species were available and examined. Of the seven yellow-spored taxa originally described for Australia, six fell into one of either three distinct groupings corresponding to the three species: *Phaeoceros carolinianus*, *P. evanidus*, and *P. inflatus*. Unfortunately, of the remaining taxon, neither the lectotype nor the isolectotype of *Phaeoceros tuberosus* (Taylor) Prosk. that we have seen to date had mature sporophytes, though morphologically the gametophyte clearly falls at the very least within the order Notothyladales Hyvönen & Piippo. Speculation as to which genus it might fall under and the need to examine fertile type material has required us to leave *P. tuberosus* out of this paper at present. Tubers described for all four taxa in this paper are typical of those found in *P. pearsonii* (M. Howe) Prosk., which are ventral, subterminal, and without stalks.

Descriptions are given of all three species, as well as of a new species, *P. engelii*. A list of distinguishing features is given in Table 1.

Phaeoceros Prosk., Bull. Torrey Bot. Club 78(4): 346 (1951)

ETYMOLOGY—From the Greek *phaeo-* (dark) and *ceros* (a horn), in reference to the dark coloring and shape of the mature sporophyte.

TYPE—*Phaeoceros laevis* (L.) Prosk.

A widely occurring genus in both the Northern and Southern hemispheres *Phaeoceros* consists of ca. 40 taxa, of which *Phaeoceros carolinianus* (Michx.) Prosk. and *P. laevis* are the most widespread species worldwide (Hässel de Menéndez, 1987; Schuster 1992). Distinguishing characters for the genus in Australia include smooth solid thallus, yellow spores, irregularly arranged jacket cells of the antheridia, and possession of tubers in some species.

Phaeoceros carolinianus (Michx.) Prosk. Bull. Torrey Bot. Club. 78: 347. 1951

Basionym—*Anthoceros carolinianus* Michx. *Flora Boreali-Americana* 2: 280. 1803. Type: USA. Carolina inferiori, herb. Camus, herb. Richard (holotype in PC).

Synonyms—*Anthoceros australiae* Beauv. ex Steph. Spec. Hepat. 6: 571 (1924) syn. nov. Type: Australia, New South Wales, F. v. Mueller (as *A. crispus*) (lectotype G!).

Anthoceros brotheri Steph. Hedwigia 32: 141 (1893) syn. nov. Type: Australia, Queensland, Brotherus 859 (lectotype in G!).

Anthoceros communis Steph. Bull. Herb. Boissier 5: 86 (1897). Type: Japan, Akita, Faurie 1484 (lectotype in G!) NSW 261411.

Anthoceros multicapsulus Steph., Spec. Hepat. 5: 991 (1916) syn. nov. Type: Lord Howe Island. (lectotype in G!).

Thallus transparent, yellow-green to dark green (RHS Colour chart 135D; 137B,C, and D; 144B) growing on soil or rock. Plants small to medium in size, up to 20 mm in length and 15 mm in width, forming fans, rosettes, patches or mats, adhering to bare soil or rock. Furcate to irregularly branched, frequently with ventral unstalked tubers becoming broad and flat, full of starch granules. Thallus solid, 8–12 cells thick in transverse section, varying from biconvex to plano-concave to concave-convex. Dorsal epidermal cells quadrate to hexagonal, 17–83 × 17–48 µm. Internal cells 26–82 × 26–70 µm. Ventral clefts observable sometimes and flanked by two cells. *Nostoc* colonies scattered through ventral half of thallus, appearing as dark dots. Rhizoids ventral, hyaline, or pale brown.

Monoicous, androecium with 2–5 antheridia per cavity, jacket cells irregularly arranged, $256 \times 133 \mu\text{m}$, stalk up to $38.4 \mu\text{m}$ long. Involucre erect, conical-cylindrical, up to 6 mm long, contracted at the mouth, 5–7 cells thick in transverse section. Sporophyte capsule up to 80 mm long, exserted, opening by two valves becoming twisted with drying, with well-developed columella, becoming yellow and then dark brown with age from the apex down. Assimilative layer 4–5 cells thick and sporogenous layer of two rows of spores. Epidermal cells of capsule elongated rectangular, $99\text{--}227 \times 16\text{--}22.5 \mu\text{m}$, walls becoming thickened with maturity, stomata present in the capsule wall. Spores bright yellow, rounded-tetrahedral equatorial diameter $36\text{--}43 \mu\text{m}$. Distal face covered with numerous spines, proximal face finely rugose with button-shaped verrucae confined to the center of each triradiate face. Proximal face with a distinct triradiate mark, covered in a

sculpturing of small bacillar and button-like papillae along its length. Pseudoelaters thin walled, up to 5 cells in length, frequently branched, $43\text{--}199 \mu\text{m}$ long and $9.5\text{--}22 \mu\text{m}$ wide, pale brown.

ETYMOLOGY—The species epithet “*carolinianus*” refers to the location of the type collection, which was originally collected in North (or ?South) Carolina, USA.

DISTRIBUTION AND ECOLOGY—A ubiquitous species across Australia, it is typically found growing on bare soil, on and beside bush tracks, roadside banks and banks of waterways (Fig. 1a).

AFFINITIES AND DIFFERENTIATION—*Phaeoceros carolinianus* (Fig. 2) is closely related to *P. laevis*, with many Australian collections identified as *P. laevis*; however, sexual condition and spore proximal patterns distinguish these two species. *Phaeoceros carolinianus* is monoicous and



FIG. 1. Gametophyte and sporophytes of the four Australian species of *Phaeoceros*. (a) *Phaeoceros carolinianus* (Cargill & Fuhrer 841, Queensland); (b) *Phaeoceros evanidus* (Cargill & Fuhrer 875, Queensland, Millstream Falls NP); (c) *Phaeoceros inflatus* (Cargill & Fuhrer 475, Victoria, Warrandyte SP); (d) *Phaeoceros engelii* (Cargill & Fuhrer 1017, Victoria, Lower Glenelg NP, Moleside Crk.) Scale = 10 mm.

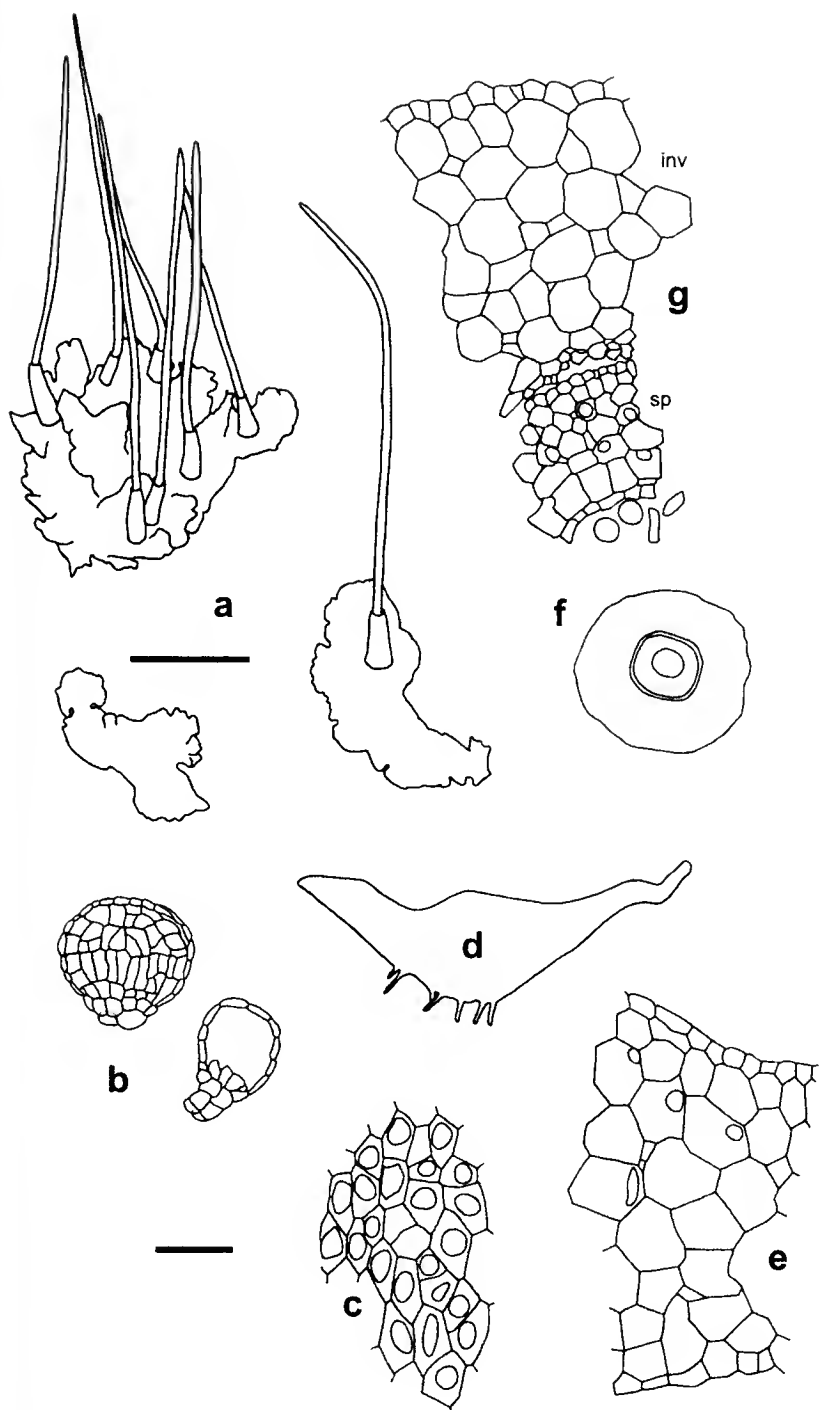


FIG. 2. *Phaeoceros carolinianus*. (a) Gametophytes with sporophytes. Scale = 4 mm. (b) Antheridia illustrating the irregular arrangement of jacket cells typical of the genus. Scale = 100 μ m. (c) Dorsal epidermal cells of thallus. Scale = 100 μ m. (d) Transverse section (TS) of thallus. Scale = 100 μ m. (e) Cells of thallus through TS section. Scale = 100 μ m. (f) TS through basal section of sporophyte and involucre. Scale = 100 μ m. (g) Internal cells of sporophyte; inv = involucre; sp = sporophyte. Scale = 100 μ m.

proximal verrucae numbers are low and confined to the central section of each triradiate face (Fig. 3). The type spores of *P. laevis* have verrucae covering each of the triradiate faces and it is dioicous (Proskauer, 1951; Hässel de Menéndez, 1987). *Phaeoceros laevis* has not been confirmed to occur in Australia, and is probably confined to the northern hemisphere.

SPECIMENS EXAMINED—Australian Capital Territory: Head of Murray's Gap, Bimberi Ra., Cotter River District, mud banks in swampy herb field, *Schodde* (AD 26972); Gladfield, Darling Downs, *Gwyther* 331871 (BRI); Bendoura Dam Rd., Brindabella Ra., 28 km SW of Canberra, *Streimann* (CBG 7804945); Little Collins

Crk., Brindabella Ra., head of small shaded gully. *Streimann* 5281 (CBG 7804939); Botanic Gardens, Canberra, common on moist, shaded stream banks, *Streimann* (CBG 066486); Murray's Beach, Jervis Bay, wet shaded cliff face above beach, *Streimann* 5032 (CBG 7892211); Bull's Head, Brindabella Ra., on moist earth, on rock outcrop in Eucalyptus forest, *Scott s.n.* (2) (MUCV129). **Lord Howe Island:** Lord Howe Is. (MEL 1039116, 1039117, 1039126 & 1039127); 1 km E of King's Beach at foot of Mt. Lidgbird, on bank of creek, *Corrick* 11049 (MEL 11049). **New South Wales:** Minyon Falls, 25 km NNE of Lismore, moist exposed rocks below falls, *Streimann* 6844 (CBG 7905590); Wilson's Crk., 8 km W of Mullumbimby, on rocks beside stream, *Bender* 14 (CBG 7708512); Flat Rock Crk., North Shore, Sydney, wet banks, *Whitelegge s.n.* (MEL 1039092); Mossmans Bay, near Sydney, waterfalls, *Watts* 199 (as *Anthoceros communis* NSW 261411); Centennial Park, Sydney, *Cheel* 803 (as *Anthoceros brotheri* NSW 261409); between Mt. Kiera & Wollongong, moist soil, on the roadside, *Coveny s.n.* (NSW 261536); Gosford Rd. near Woy Woy, rocks by waterfall, *Bessie* 1/59 (SYD); Huntley Point, *Barnard s.n.* (SYD BARN 4.11.25); Somersby Falls, *Na-Thalang s.n.* (SYD O.N.T. 2.7.66(1)); Nadgee Fauna Reserve, between W Newtons Beach and Little River, on soil on bank of gully, *Hewson s.n.* (SYD HJH 18.4.65 (1)). **Norfolk Island:** Broken Bridge Crk., on continuously wet overhanging rock, *Hoogland* 6632 (CANB 77819). **Queensland:** Mooloolah River, 2 km SW of Mooloolah, Moreton District, on peaty detritus among rocks in bed of running stream, *Windolf* 124 (BRI 331874); Warrumbah Crk., Carnarvon Nat. Park, narrow shaded gorge with scattered shrubs and trees, on semi-exposed rocks in creek, among *Lunularia*, *Steimann* 52188 (CBG 9312854); Murphey's Crk., 16 km NE of Toowoomba, side of creek on rocks, dry sclerophyll forest, *Streimann* 370 (CBG 051234); Kin Kin Crk., 19 km NNW of Tewantin, creek bank, sandy loam, *Telford* 4341 (CBG 7902323); Johnstone River track near Sutties Crk., Tully, on roadside bank, tropical rainforest, *Scott s.n.* (MELU 6743); Blencoe Crk., Kiirama State Forest, Cardwell, riverbank, cleared tropical rainforest, *Scott s.n.* (MUCV 6924) Millstream Falls, Ravenshoe, on bare soil at side of track, *Cargill & Fuhrer* (MUCV 7991); Wright's Crk. Rd., Lake Eacham Nat. Park, on roadside bank, *Cargill* 55103 & 55104 (MUCV 7980 & MUCV 7981); Greene's Falls, S of Mt. Glorious, in rainforest, on wet rocks at top of waterfall, *Smith & Tindale* H62 (NSW 261553); Millstream Falls, Ravenshoe, *Watts s.n.* (NSW 261550). **South Australia:** Back Valley, off Inman Valley, Southern Lofty Region, *Cleland* 51 (AD 5889); Back Valley Southern Lofty Region, *Cleland s.n.* (AD 6000); Ashbourne Area, Southern Lofty Region,

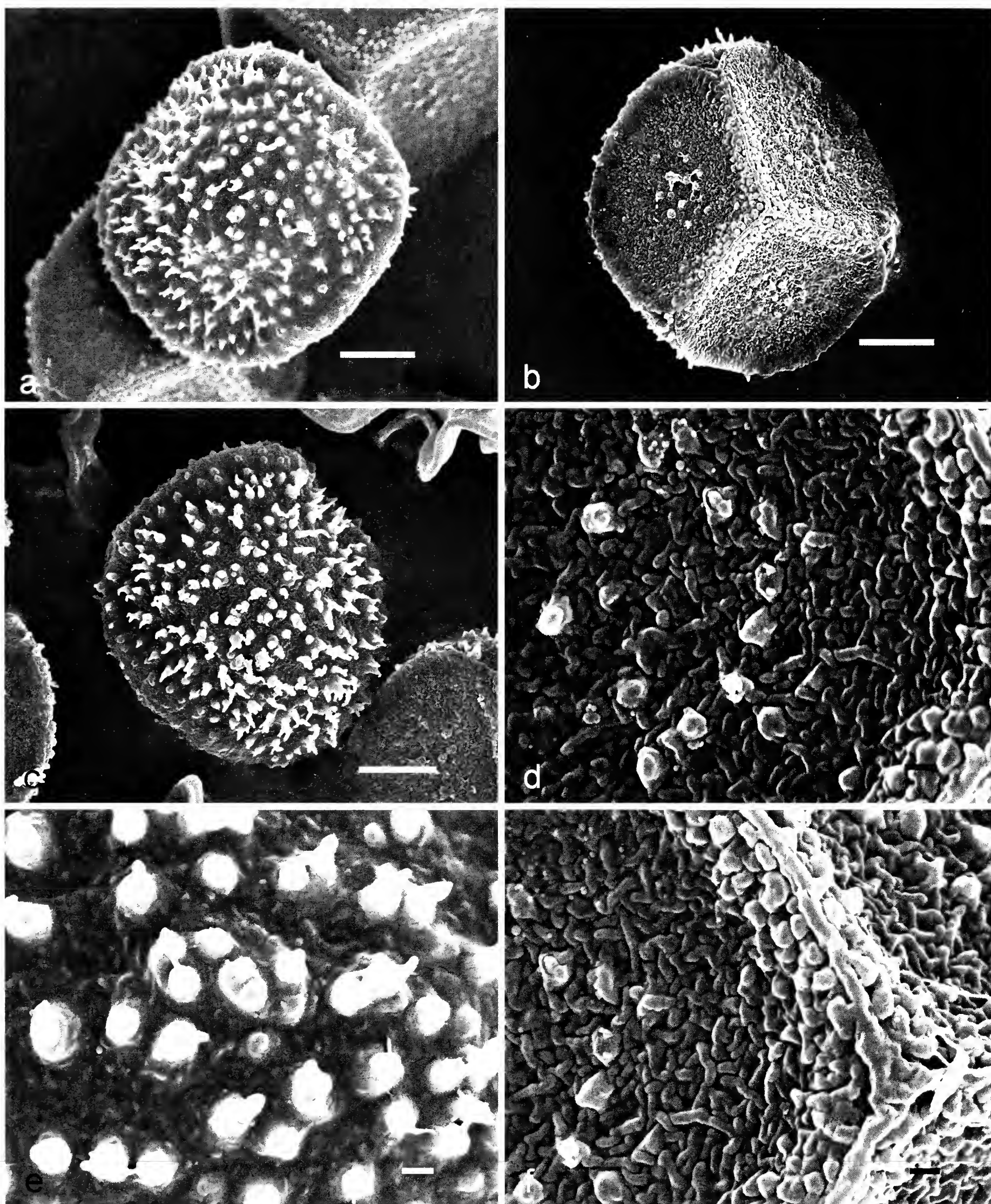


FIG. 3. SEM micrographs of spores of *Phaeoceros carolinianus*. (a, c) Distal face; (b) proximal face; (d, f) detail of proximal micro-ornamentation; (e) close-up of micro-ornamentation of distal face. Scales: (a–c) 10 μ m; (d–f) 1 μ m. [a–f from Cargill & Fuhrer 490, Australia. Victoria. S E Gippsland, Costicks Weir, Mundic Crk.]

growing on spongy ground near *Juncus* sp. and *Callitrix stagnalis*, soakage start of creek, Murfet 668 (AD 27625); Square Waterhole near Mt. Compass, in a swamp, Symon s.n. (AD 6923). **Tasmania:** Norfolk Island,

Robinson (MEL 1039122). **Victoria:** Black Spur, Bastow s.n. (MEL 1039095); Buffalo Ra. F. von Mueller s.n. (MEL 1028292); Spring Gully at Maliuns, 52 km N of Orbost on the Bogong Hwy. Thiele 709 (MELU 2452). **Western**

Australia: Worriga Gorge, Drysdale River Nat. Park, on wet sandstone rocks in shaded part below waterfall, *George 14100* (MEL 1023878); Sandy Crk., King Leopold Ranges, Kimberleys, in peaty creek bed, *Scott s.n.* (MELU 789); Galvans Gorge, West Kimberleys, damp earth among ferns, under fall of water, *Willis s.n.* (MELU 547).

***Phaeoceros evanidus* (Steph.) Cargill & Fuhrer
comb. nov.**

Basionym—*Anthoceros evanidus* Steph., Spec. Hepat. 5: 990 (1916). Type: Australia, Port Denison, *W.W. Birch* (lectotype in G!).

Thallus pale transparent yellow-green to green (RHS Colour Chart 143C, 145B), delicate, growing in rosettes on bare moist soil patches. Plants small up to 15 mm long and 2.4–15 mm wide, from single lingulate thallus to \pm fan-shaped branched thallus with overlapping lobes originating from a persistent, narrow strap posteriorly, furcately branched. Margins irregularly crenulate to \pm entire, sometimes lateral margins curving upward becoming canaliculate. Thallus solid, but some plants occasionally with large inflated epidermal cells giving the plant a “quilted” appearance typically seen in members of the Anthocerotaceae s. str. Thallus concave-convex to plano-convex in transverse section, 7–11 cells thick. Dorsal epidermal cells quadrate to hexagonal, $28\text{--}92 \times 19\text{--}53.3 \mu\text{m}$. Cells with single chloroplast and pyrenoid. Some populations with dorsal stalked obpyriform to obovoid-shaped propagules ($583\text{--}1,000 \times 473\text{--}500 \mu\text{m}$). Surface of propagules crenulate because of bulging epidermal cells. Stalk up to $1000 \mu\text{m}$ long and $500 \mu\text{m}$ wide, composed of rectangular cells with single orange chromoplast. Plants sometimes with ventral unstalked tubers. Ventral clefts flanked by two cells at apical notch. *Nostoc* colonies scattered through thallus, appearing as dark dots. Rhizoids hyaline along ventral surface.

Monoicous, androecia scattered over dorsal surface, 1–4 antheridia per cavity, spherical yellow-orange, on short stalks, $115\text{--}132.5 \times 82.5\text{--}100 \mu\text{m}$, jacket cells irregularly arranged. Involucre erect and cylindrical, contracted at the mouth, 1.2–2.8 mm long, 4–10 cells thick. Capsules erect, 5–12 mm long, exserted, splitting by two valves, assimilative layer 4–7 cells thick in transverse section, sporogenous layer 2 cells thick, with well-developed columella. Epidermal cells of capsule elongate rectangular ($66\text{--}143 \times 8.5\text{--}19.2 \mu\text{m}$)

punctuated with stomata ($33 \times 21 \mu\text{m}$). Spores bright yellow, rounded-tetrahedral, with smooth border, equatorial diameter from $32\text{--}49 \mu\text{m}$. Distal surface with numerous coarse, wart-like protuberances, frequently coalescing in the center of the face, with smaller scattered verrucae in between larger protuberances, equatorial girdle smooth. Proximal surface with distinct triradiate mark covered in small spherical to baculate papillae on either side of a narrow, smooth dehiscence line. The three triradiate faces of the proximal surface covered with distinct button-like verrucae. A distinct shallowly papillate margo encircles the entire proximal face. Pseudoelaters 1–3 cells, $36\text{--}164 \times 9.5\text{--}33 \mu\text{m}$, pale brown, thin-walled, occasionally branched.

ETYMOLOGY—The species epithet “*evanidus*” in Latin means vanishing. Stephani was probably referring to the ephemeral nature of this species.

DISTRIBUTION AND ECOLOGY—This species is confined to the tropical northeastern region of Australia from the Atherton Tablelands of Far North Queensland to northern New South Wales.

AFFINITIES AND DIFFERENTIATION—Possibly overlooked because of small size of plants (Fig. 1b), it is distinguished from both *P. carolinianus* and *P. inflatus* by its distinct spore patterning (Fig. 5). The spore distal face of the former species is covered in spine-like protuberances, whereas that of the latter species displays fewer, less coarse protuberances. Both species also lack the number of distinct button-like verrucae covering each of the triradiate faces. The proximal micro-ornamentation between verrucae is lacking in *P. evanidus*, whereas it is composed of interwoven vermiculae for both *P. carolinianus* and *P. inflatus*. It is also distinguished from *P. inflatus* by its monoicous sexual condition (Fig. 4).

SPECIMENS EXAMINED—**New South Wales:** Duck Creek Rd., 22 km WNW of Bulahdelah, disturbed clearing beside road at edge of forest dominated by *Eucalyptus*. *Curnow 3304* (CBG 9313538); New South Wales. *Leichardt s.n.* (MEL 1039120). **Queensland:** Port Denison [Qld]. *W.W. Birch s.n.* (lectotype G 2107/5); Charleys Creek, 18 km NNE of Proserpine, poor, scrubby forest on rocky hillside, on soil. *Curnow 1160* (CANB 753174); Millstream Falls NP, on bare soil on side of walking track down to lookout *Cargill & Fuhrer 875, 876* (CANB 753175, CANB 753176); Queensland. *Bowmann* (MEL1039123) Millstream Falls, Ravenshoe, on bare soil on side of walking track. *Cargill 55100* +

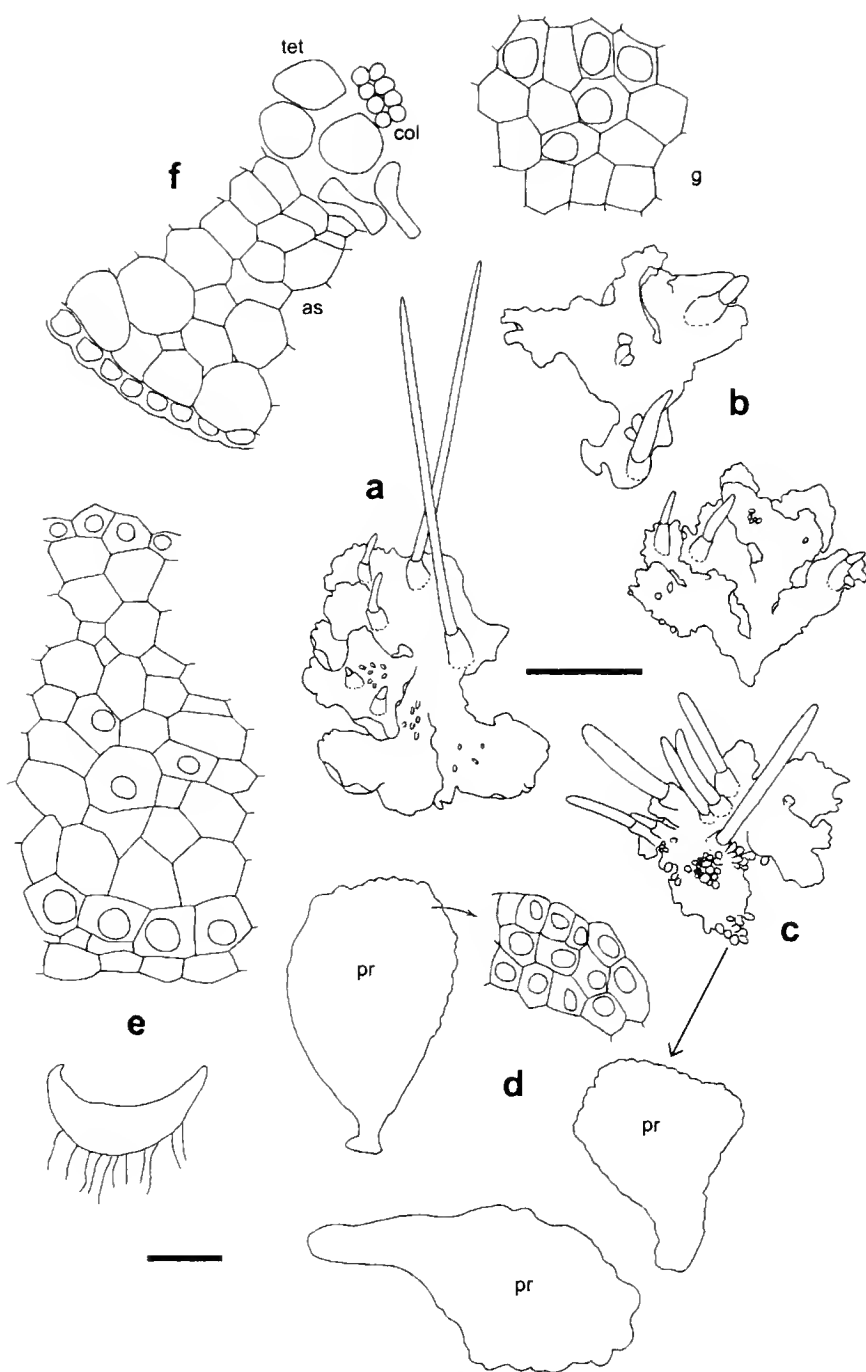


FIG. 4. *Phaeoceros evanidus*. (a–b) Gametophytes with sporophytes. (a) Scale = 4 mm; (b) two plants, scale = 3 mm; (c) gametophytes with sporophytes and propagules, scale = 5 mm; (d) propagules (pr), scale = 100 µm, and epidermal cells of propagules; (e) transverse section through thallus displaying a concave-convex shape, scale = 100 µm, and internal cells of thallus; (f) TS through sporophyte (as = assimilative layer, col = columella, te = tetrads); (g) dorsal epidermal cells of gametophyte thallus. All cell illustration scales = 100 µm.

dupl. (MUCV 7986 & MUCV 7987); Broadwater Forest Park, W. of Ingham, *Stone s.n.* (MELU 1084)

***Phaeoceros inflatus* (Steph.) Cargill & Fuhrer comb. nov.**

Basionym—*Anthoceros inflatus* Steph., Spec. Hepat. 5: 990. 1916. Type: Australia, New South Wales, Uralba, *W. W. Watts 391* (lectotype in G!, isotype in NSW!).

Thallus bright green to yellow-green to olive green (RHS Colour Chart: males 144A, B; females 143B), becoming brown when dried, growing on soil or rocks in mats or rosettes. Female plants

small to medium in size, up to 20 mm in length and 5 mm in width, irregularly branched, apices of branches spatulate. Thallus solid, 8–9 cells thick, usually concave-convex, fleshy. Margins of plants entire, undulate or irregularly crenulate. Dorsal epidermal cells rectangular to hexagonal, $28\text{--}79 \times 20\text{--}56 \mu\text{m}$. Plants frequently with ventral unstalked tubers. Ventral clefts not observed. *Nostoc* colonies scattered through the ventral portion of thallus as dark dots. Rhizoids ventral and hyaline or pale brown.

Dioicous, male plants smaller, up to 10 mm long and 2 mm wide. Androecium with (1–)2–3 antheridia per cavity, ovoid to spherical, white to bright yellow, sunken into thallus, $163\text{--}250 \times 133\text{--}150 \mu\text{m}$ on short stalks, cells of jacket irregularly arranged. Involucres erect cylindrical, up to 4 mm long. Capsules up to 40 mm long, one per involucre, splitting on either one or two sides by way of two valves, frequently remaining attached at apex, stomata scattered throughout epidermal layer, $61\text{--}77 \times 41\text{--}51 \mu\text{m}$, assimilative layer 5–7 cells thick in transverse section, sporogenous layer 1–2 tetrad layers thick, with well-developed columella. Epidermal cells of capsule rectangular to hexagonal and elongate $59\text{--}187.5 \times 15\text{--}30 \mu\text{m}$. Spores yellow to yellow-grey, $37.5\text{--}56.5 \mu\text{m}$ in diameter, rounded-tetrahedral. Distal surface with irregularly scattered, coarse protuberances, variable in shape crowned with one to several blunt triangular-shaped, wart-like or tuberculate papillae, never spine-like, intervening surface wrinkled, finely papillate or nearly smooth. Proximal surface with distinct, broad triradiate mark, entire face surrounded by a distinct cingulum. Triangular faces, flat or concave, with fine interwoven vermiculate-like patterning on surface, verrucae confined to central section of each face and can be distinct or indistinct. Pseudoelaters pale brown to dark brown at maturity, transparent, thin-walled and 1–4 celled, $(41\text{--})46\text{--}297 \mu\text{m}$ in length and $7.5\text{--}28(38.4) \mu\text{m}$ in width, linear or branched.

ETYMOLOGY—The species epithet “*inflatus*” arises from Stephani’s observation of an inflated assimilative layer within the capsule resulting in a bulging involucre (see Stephani’s *Icones Hepaticarum*).

DISTRIBUTION AND ECOLOGY—A relatively common species among the Australian anthocerotales, extending down the eastern area of Australia from Queensland down to Victoria.

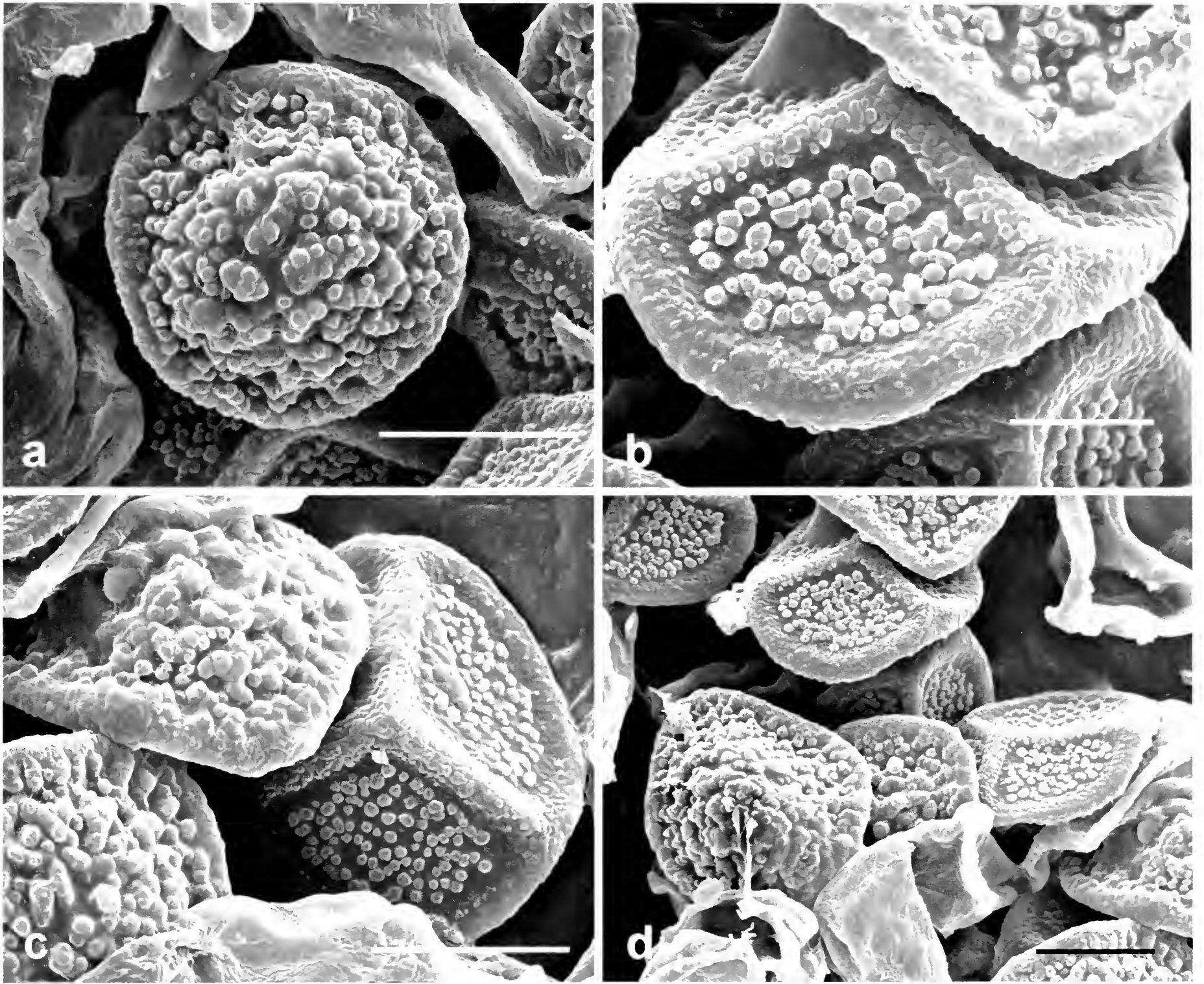


FIG. 5. SEM micrographs of spores of *Phaeoceros evanidus*. (a) Distal face; (b) one of the triradiate sections of proximal face; (c) proximal face and equatorial view of spores; (d) group of spores and pseudoelaters. All scales = 20 μ m, except (b) = 10 μ m. [a–d from type of *Anthoceros evanidus* (G)]

Typically found growing on moist soil of banks and pathways, often in shaded habitats.

AFFINITIES AND DIFFERENTIATION—Stephani described this species from a specimen sent to him by Rev. W. W. Watts from the Richmond River at Uralba, NSW (Stephani, 1916). His description of this taxon is somewhat confusing, in that he has described the thallus “cavernosa” which is typical of *Anthoceros* s. str.; yet, he is clear that the spores are pale yellow and minutely papillate. Examination of the type specimen confirms its placement within the genus *Phaeoceros* with possession typically of a solid thallus, irregularly arranged jacket cells of the antheridia and yellow spores. It differs from both *P. carolinianus* and *P. evanidus* in its dioicous sexual condition and irregular coarse protuberances topped by smaller,

irregular-shaped papillae observed on the distal face of the spores (Figs. 1c, 6, 7).

SPECIMENS EXAMINED—**Australian Capital Territory:** Head of Murray’s Gap, Bimberi Range, on mud banks in swampy herb. field. *Schodde 1302* (NSW 261525 & CANB 108656). **New South Wales:** Richmond River, Uralba, on ground, hill top, 23 September 1901. *W. W. Watts n. 371* (lectotype G! : isotype NSW 261462!); Hurstville, near Sydney, on earth. *Whitelegge* (NSW 259158); North Shore, Sydney. *Whitelegge* (NSW 259155); NSW 261701; Hurstville near Sydney. *Whitelegge* (MEL 1039090); North Shore, Sydney. *Whitelegge s.n.* (MEL 1039191). **Queensland:** Flinders River (MEL 1039114). **Victoria:** Near Dimboola. *Willis s.n.* (MEL 1039091); end of forest road to Hogan’s Flat, above Lerderderg River Gorge (and opposite Mt.

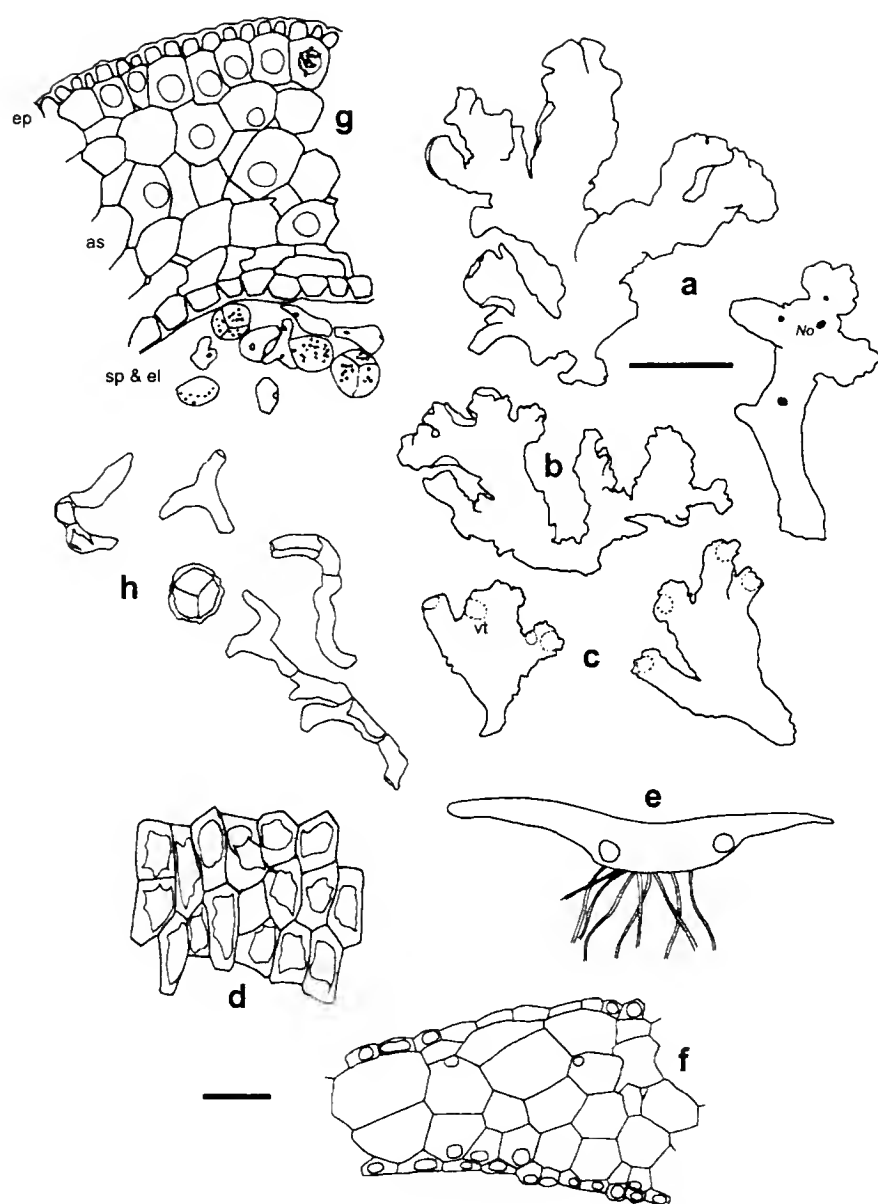


FIG. 6. *Phaeoceros inflatus*. (a–c) Female gametophytes (No = *Nostoc* colonies), scale = 3 mm; (b) scale = 4 mm; (c) scale = 5 mm (vt = ventral tuber); (d) dorsal epidermal cells, scale = 100 μ m; (e) TS through thallus, scale = 100 μ m; (f) internal cells of thallus, scale = 100 μ m; (g) TS through sporophyte (ep = epidermal cells, as = assimilative layer, sp = spores; el = pseudoelaters); (h) mature spore and pseudoelaters, scale = 100 μ m.

Blackwood), Blackwood Ranges. *Willis s.n.* (MEL 1030295); Anderson Inlet, (MEL 1039119); Heathermere Siding Rd., Heathermere, *Cargill & Fuhrer 17733* (MELU 6368); Yeodene, SE of Colac, *Beauglehole 1965* (MEL 1043437); Belgrave Sth camping ground, on moist clay bank beside lake, *Scott s.n.* (MUCV 367); Whitehills Dam, Rushworth, *Scott s.n.* (MUCV 4787); Yarra Glen-Yea Rd. (west side), on damp clay bank, under trees, *Scott s.n.* (MUCV 4328); Main Ridge, Mornington Peninsula, on clay soil in *Eucalyptus obliqua* forest, *Scott s.n.* (MUCV 2561); Scott's [farm] block, Frazer River, King Island, *Scott s.n.* (MUCV 4022); Jumping Creek, Warrandyte SP, carpark, on bare soil at side of road, *Cargill & Fuhrer 55014, 55015, 55030* (MELU 7917, 7922, 7916); Silverband Falls, Grampians Nat. Park, at base of walking track on earth bank, *Cargill & Fuhrer 55022, 55025, 55027, 55028, 55029* (MUCV 7906, 7911, 7913, 7914, 7915); Mt. Victory Rd. near Hall's Gap, Grampians Nat. Park, rocky alcove on side of road in deep shade, *Cargill & Fuhrer 55020* (MUCV 7903).

***Phaeoceros engelii* Cargill & Fuhrer sp. nov.**

Type—Australia. Victoria. Lower Glenelg National Park. Kentbruck Rd. bridge over Moleside Crk. 11 October 2006. *Cargill & Fuhrer 1016* (Holotype CANB).

Ab omnibus aliis speciebus *Phaeoceratis* propagulis numerosis habens praeter margines thalli, coloniis *Nostocinis* ventralibus tumescentibus, et propriis eminentia trabeculatis in pagina distali sporarum, differt.

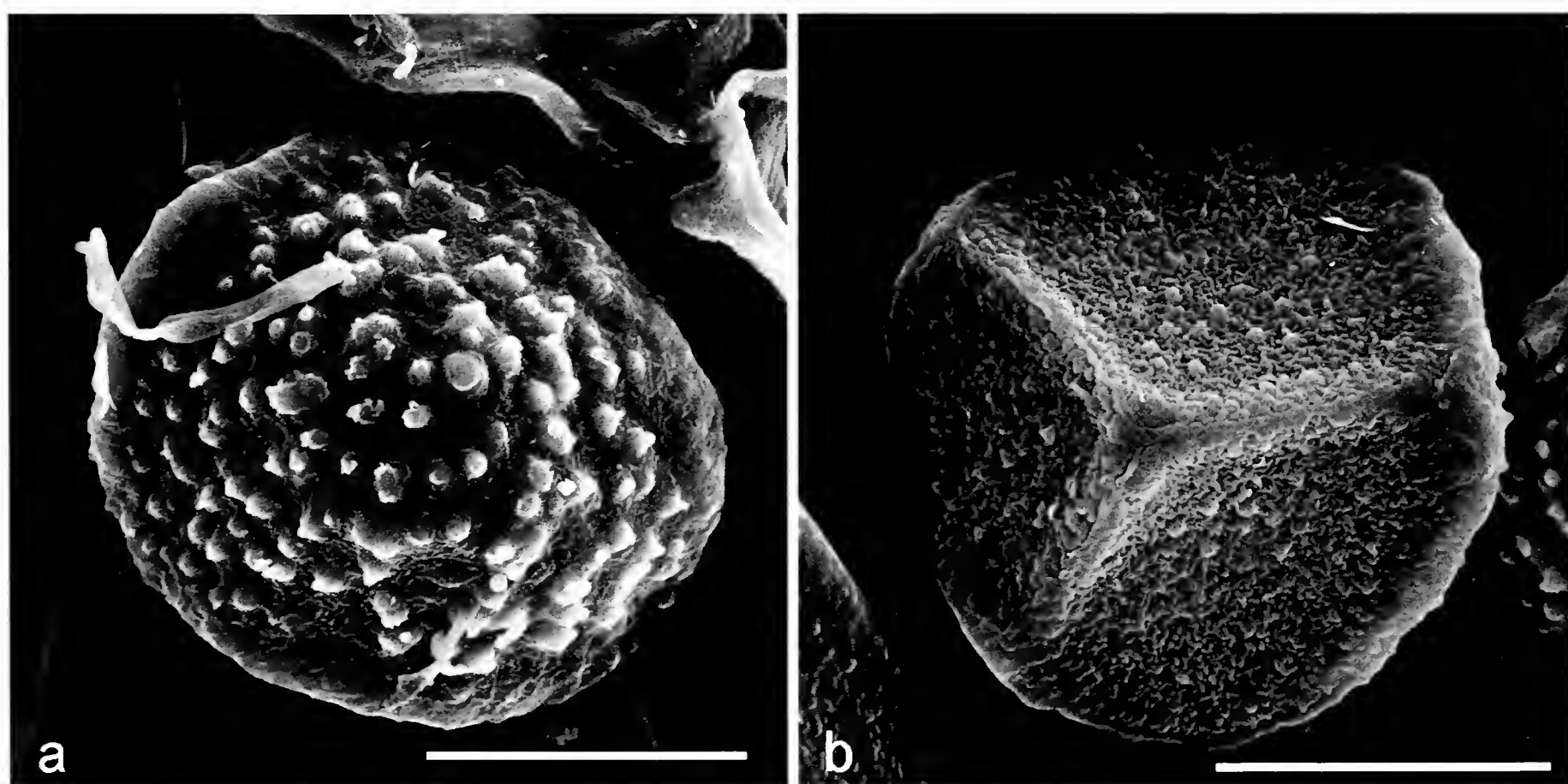


FIG. 7. SEM micrographs of spores of *Phaeoceros inflatus*. (G): (a) Distal face; (b) proximal face. Scale = 20 μ m. [a, b from type of *Anthoceros inflatus* (G)]

Thallus yellow-green (RHS Colour Chart 146A), but appearing dark green at habitat because of deep shade and becoming black-green when dried, growing on soil or rocks in mats close to edge of creek or on rocks in creek or on banks of creek. Female plants up to 60 mm long and up to 11 mm wide, irregularly furcate branching, frequently with young lateral branches forming on mature thallus, lobes lingulate at apices. Thallus solid, 8–13 cells thick, plano-convex to concave-convex in transverse section, fleshy. Margins of thallus irregularly crenulate, with some populations possessing margins fringed with deciduous propagules. Dorsal epidermal cells quadrate to hexagonal, $25\text{--}57.5 \times 22.5\text{--}37.5\text{ }\mu\text{m}$. Thickening of ventral apices observed in plants not unlike the ventral unstalked tubers typically seen in this genus. No ventral clefts observed. *Nostoc* colonies scattered through thallus becoming spherical and bulging significantly from ventral surface with maturity. Rhizoids ventral and pale brown.

Dioicous, male plants smaller, up to 21 mm long and 4 mm wide. Androecium with 2 antheridia per cavity, ovoid, pale yellow, sunken into thallus, $175\text{--}325 \times 150\text{--}240\text{ }\mu\text{m}$, on short stalks, jacket cells irregularly arranged. Involucres erect, cylindrical, flaring at base up to 5 mm long, 5–8 cells wide in transverse section. Capsules up to 30 mm long, one per involucre, exserted, becoming blackish brown at tips with maturation of spores, opening by two valves, 6–8 cells thick in transverse section, stomata scattered throughout epidermal layer, $72.5\text{--}90 \times 42.5\text{--}60\text{ }\mu\text{m}$. Epidermal cells of capsule rectangular to hexagonal and elongate $82.5\text{--}170 \times 12.5\text{--}27.5\text{ }\mu\text{m}$. Spores yellow, $38\text{--}56.3\text{ }\mu\text{m}$ in diameter, rounded-tetrahedral. Distal surface covered in short irregular trabeculate protuberances frequently coalescing to form irregular lamellae. Proximal surface covered in numerous irregular-shaped verrucae. Pseudoelaters pale brown at maturity, transparent, thin-walled and 1–4-celled, linear or branched, $67\text{--}223\text{ }\mu\text{m}$ in length and $15\text{--}23\text{ }\mu\text{m}$ in width.

ETYMOLOGY—Named for Dr. John Engel to commemorate his 40 years in hepaticology.

DISTRIBUTION AND ECOLOGY—This species is known only from one location beside and within a creek in the Lower Glenelg National Park. Its habitat preference is very similar to that of most *Megaceros* populations in relatively shady conditions near running water. In fact, when first collecting this hornwort, we had thought that it was indeed a *Megaceros*.

Subsequent maturation of the sporophytes and examination of the spores placed it squarely in the genus *Phaeoceros*.

AFFINITIES AND DIFFERENTIATION—Collections made in later years revealed plants with numerous deciduous propagules growing almost like a fringe around the margins of the thallus (Figs. 1d, 8a). They are also found growing in patches on the dorsal and ventral surfaces of the thallus. Not infrequently, it would appear that some propagules remained attached to the parent thallus and grow to produce secondary branches. Similar structures were also observed and described by Howe for the species *Anthoceros vegetans* M. Howe (Howe, 1934) and by Stephani for the Chilean species *P. propaguliferus* (Steph.) Prosk. (Stephani, 1917). Also peculiar to this species is the morphology of the mature *Nostoc* colonies, which bulge out as a relatively large hemispherical growth from the ventral surface of the thallus (Fig. 8c), unlike the typical colonies,

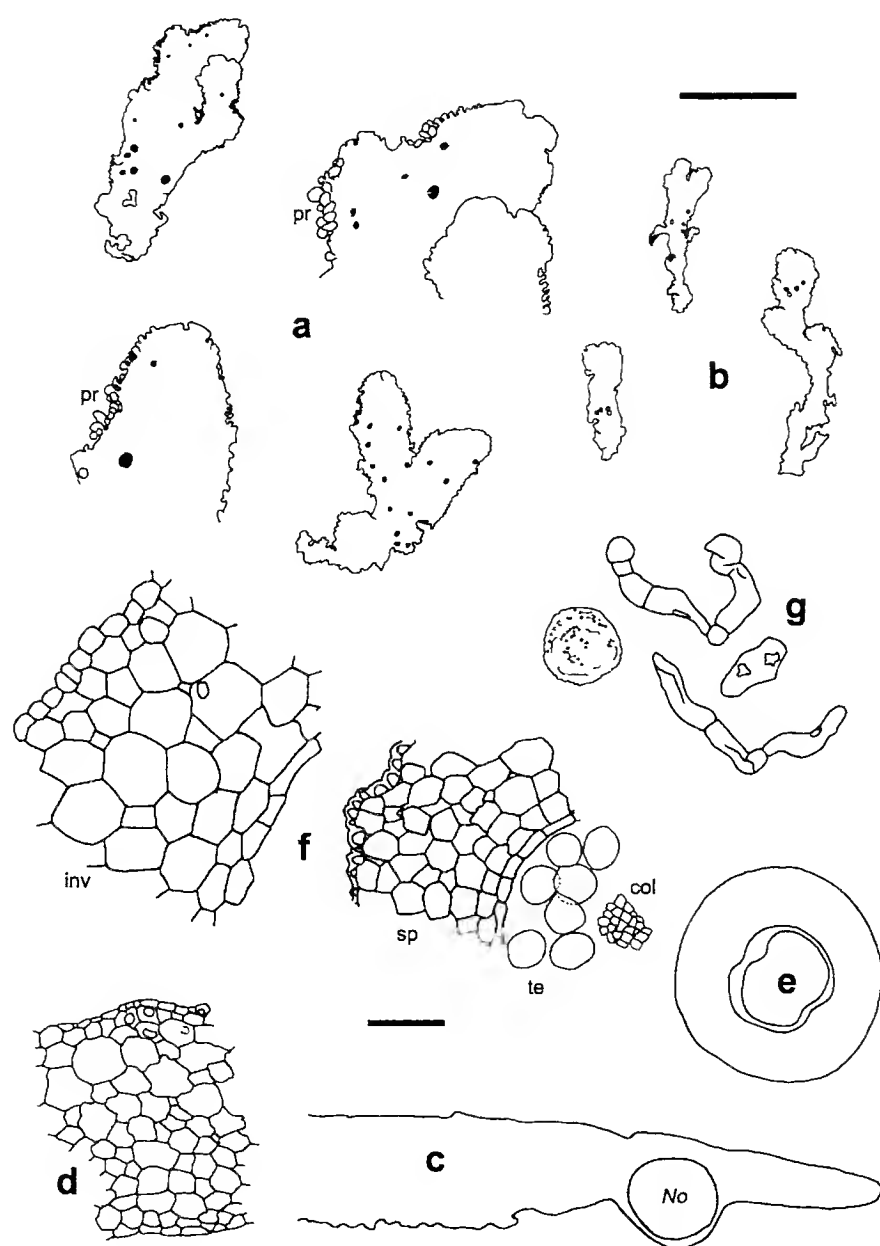


FIG. 8. *Phaeoceros engelii*. (a) Female gametophytes with marginal propagules, scale = 10 mm; (b) male gametophytes, scale = 10 mm; (c) TS through thallus illustrating *Nostoc* colony bulging from ventral surface, scale = 3 mm; (d) internal cells of thallus, scale = 100 μm ; (e–f) TS through sporophyte and involucre, (e) scale = 3 mm, (f) scale = 100 μm (inv = involucre, sp = sporophyte, te = tetrad, col = columella); (g) spore and pseudoelaters, scale = 25 μm .

which remain small and well embedded in the ventral portion of the thallus (Fig. 6e). This phenomenon has not typically been observed in other Australian species of *Phaeoceros*. The sexual condition and spore distal pattern (Fig. 9) distinguish this species from both *P. carolinianus* and *P. evanidus*, both of which are monoicous, whereas *P. engelii* is dioicous. Also, the more robust habit of the populations of *P. engelii* (Figs. 1d, 8) separates it immediately from the more diminutive *P. evanidus*.

It differs from *P. inflatus* in its possession of numerous propagules, but where these are not apparent, it differs significantly in the spore

distal patterns. The spores of *P. inflatus*, while displaying protuberances from the distal face, differ in their micro-morphology. *Phaeoceros engelii* displays trabeculate protuberances (Fig. 9), whereas *P. inflatus* displays typically fewer, coarser protuberances that are often crowned by another layer of spine-like or wart-like papillae (Fig. 7).

SPECIMENS EXAMINED—**Victoria:** Kentbruck Rd. bridge over Moleside Crk., Lower Glenelg NP. *Cargill & Fuhrer 1016* (Holotype CANB); *Cargill & Fuhrer 363* (CANB 654152); *Cargill & Fuhrer 1015*, (CANB); *Cargill & Fuhrer 1017* (CANB).

Key to the Species

- 1. Plants monoicous2
- 1. Plants dioicous3
- 2. Plants robust, up to 20 mm long, without propagules, widespread distribution, spores with spine-like protuberances over distal face*Phaeoceros carolinianus*
- 2. Plants delicate, up to 15 mm long, sometimes with dorsal propagules, restricted in distribution to tropical and subtropical areas, spores with large, wart-like, coalescing protuberances, proximal surface with distinct button-like verrucae covering each triangular face.....*Phaeoceros evanidus*
- 3. Plants dark green, often with propagules along margins of thallus and with bulging ventral *Nostoc* colonies, restricted distribution, spore distal face covered in short trabeculate protuberances frequently coalescing to form short lamellae*Phaeoceros engelii*
- 3. Plants bright green, without propagules, *Nostoc* colonies not bulging, widespread, spore distal face with scattered irregular protuberances *Phaeoceros inflatus*

TABLE 1. List of distinguishing characters of four Australian species of *Phaeoceros*.

<i>Phaeoceros</i> species	Size of plants	Color	Tuber type	Propagules	<i>Nostoc</i> colonies	Sexual condition	No. of antheridia per cavity	Spores
<i>P. carolinianus</i>	Up to 20 × 15 mm	Yellow-green to dark green	Unstalked, ventral marginal	Absent	Embedded in thallus, not bulging	Monoicous	2–5	Yellow, distal face spiney
<i>P. evanidus</i>	Up to 15 × 2–15 mm	Pale yellow-green to green	Unstalked, ventral marginal	Dorsal	Embedded in thallus, not bulging	Monoicous	1–4	Yellow, distal face wart-like
<i>P. inflatus</i>	Females; up to 20 × 5 mm males up to 10 × 2 mm	Bright green to yellow-green to olive green	Unstalked, ventral marginal	Absent	Embedded in thallus, not bulging	Dioicous	(1–) 2–3	Yellow, distal face coarsely papillate
<i>P. engelii</i>	Females up to 60 × 11 mm; males up to 21 × 4 mm	Yellow-green to green	Unstalked, ventral marginal dark	Marginal, ventral and dorsal	Ventral and bulging	Dioicous	2	Yellow, distal face trabeculate forming lamellae

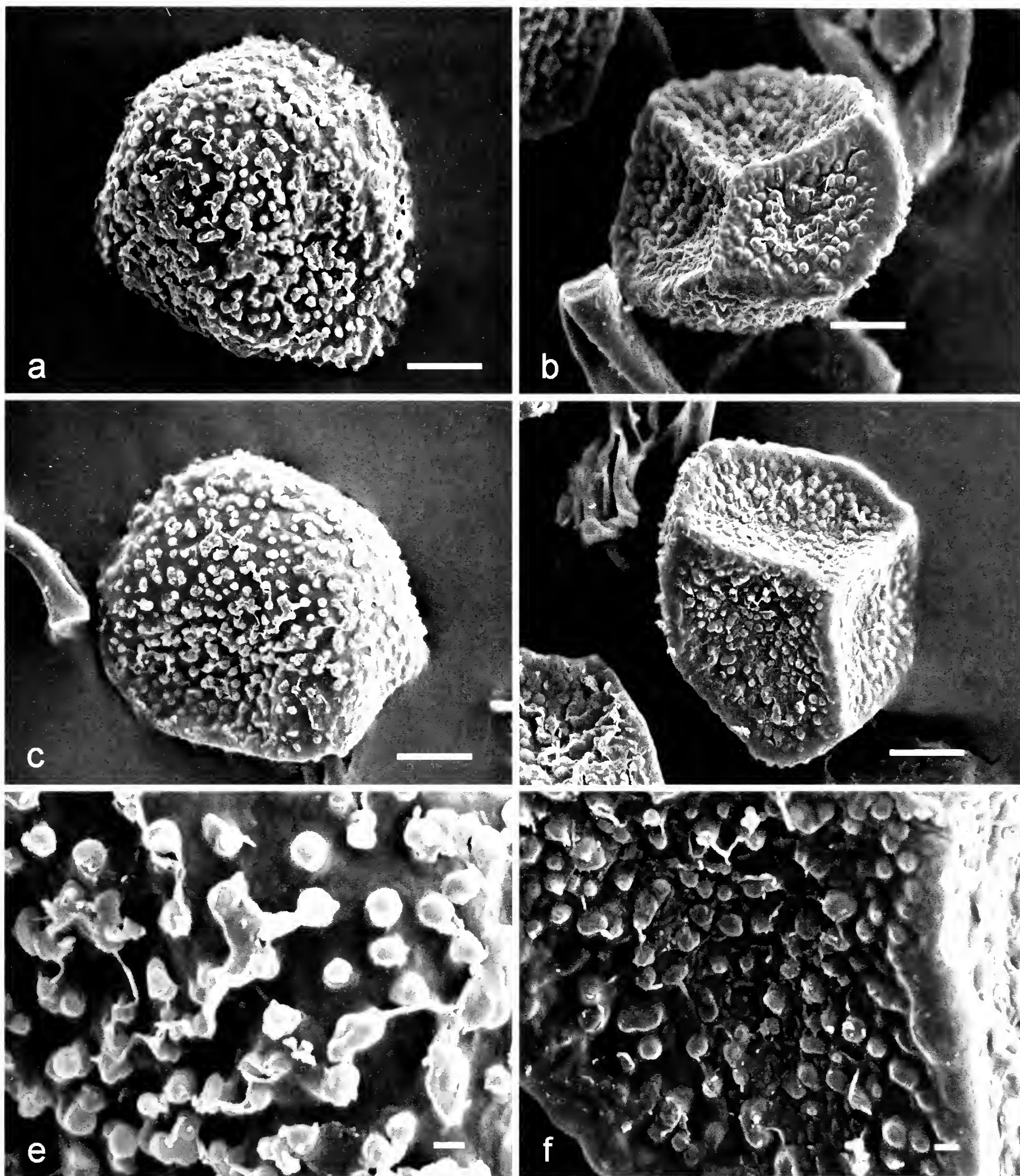


FIG. 9. SEM micrographs of spores of *Phaeoceros engelii* (a, c) distal face; (b, d) proximal face; (e) detail of micro-ornamentation of distal face; (f) detail of micro-ornamentation of proximal face. Scales (a–d) 10 μ m, (e–f) 1 μ m. [a–f Cargill & Fuhrer 363. Victoria. Lower Glenelg NP. Moleside Crk.]

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Abstract

The known and presumed origins and meanings of the accepted names of liverwort and hornwort genera known from Australia are outlined.

“The question is,” said Alice, “whether you can make words mean so many different things.”

“The question is,” said Humpty Dumpty, “which is to be master—that’s all.”

—Lewis Carroll, *Through the Looking Glass*, chapter 6

Introduction

The origins of generic names are only a curiosity to most botanists. They are more important to taxonomists, who must grapple with the intricacies of the *International Code* and classical Greek and Latin when devising new names and assessing old ones. The etymologies of names are not always

clear, particularly older names based on discarded generic concepts or constructed from unusual combinations of words, or honoring obscure friends or patrons. Many authors have neglected to explain the etymology of their new names, apparently assuming that they would be obvious to any reader interested in the matter.

Authors who have coined a large number of names have tended to follow predictable paths—many of Samuel Gray's names honor the patrons of the great Italian botanist Pier Antonio Micheli; Bethélemy Dumortier's names mostly reflect significant perianth features; many of Giuseppe Raddi's names honor Tuscan politicians or patrons; Rudi Schuster seems to prefer two-word combinations that reflect the taxonomic parentage of the type species; and Richard Spruce, in inventing names for his subgenera (now genera) of *Lejeunea*, simply added a prefix that reflected the character that best defined the subgenus. William Mitten, who named many bryophyte genera, regrettably never explained his names, many of which are very obscure.

In this paper the roots given are Greek unless otherwise stated. I have provided only the anglicized Greek words, since the original Greek would add little for most readers and can be found easily enough in a classical Greek dictionary. Where names are based on a Latinized Greek root, the Greek is given. Forms and spellings of Greek roots generally follow the monumental Greek–English lexicon of Liddell and Scott (1968), supplemented by Morwood and Taylor (2002), and Latin roots follow the classic Latin–English dictionary of Lewis (1891). Note that in some anglicized Greek roots, such as *hydros*, *hymen*, and *rhodos*, the *h* is added to indicate an aspirated accent equivalent to that letter in sound; there is no written equivalent of a pure *h* in classical Greek.

The genera treated here are those listed for Australia by McCarthy (2006) plus some others subsequently reported or known to occur there. Wherever possible I have returned to the original publication (or author) of the name in order to determine the true etymology, rather than relying on later interpretations which might be based on different generic concepts. Unfortunately I have not been able to obtain a copy of Le Jolis' paper on hepatic nomenclature (Le Jolis, 1895), which might have provided additional insights into the names discussed in this paper. However, I was able to locate the first edition of Karl Müller's *Die Lebermoose* (Müller, 1905–1911, 1912–1916) in which he gives an etymology for each generic name. I have referred to this edition rather than the more widely known third edition (Müller, 1951–1954, 1956–1958) for the sake of consistency, except where necessary to clarify a point. Where no reference is given, the interpretation is my own, for which I welcome any necessary corrections.

The *International Code of Botanical Nomenclature* (McNeill et al., 2006) fixes the first edition of *Species Plantarum* (Linnaeus, 1753) as the starting point for the names of liverwort genera and species, but many (if not most) were coined by earlier authors. It is useful to note the pre-Linnaean authors in these cases, as this often clarifies the plant character or the person to whom the name originally referred. Author names are abbreviated in accordance with Brummitt and Powell (1992), and the year of publication of the name is included to give a chronological context. For details of the places of publication of generic names, see Leussink and Stafleu (1979).

Finally, the rationales outlined here for the naming of genera are very often at odds with modern concepts of the genera, and must be viewed in their historical rather than systematic context.

Etymologies

Acrobolbus Nees 1844—*akros* (at the tip, end) + *bolbos* (bulb), alluding to the location of the marsupium at the tip of the shoot.

Acrochila R. M. Schust. 1963—*akros* (at the tip, end) + *-chila* (from *Plagiochila*), a neat combination reflecting its similarity to *Plagiochila*, from which it was separated, and the terminal perianth: “Distinctive for this genus is the *Plagiochila*-like growth-habit and perianth” (Schuster, 1963, p. 285).

Acrolejeunea (Spruce) Schiffn. 1893—*akros* (at the tip, end) + *Lejeunea*, alluding to the perianth, “which has the rare character...of being terminal on the stem, or on long branches, without any subfloral innovation” (Spruce, 1884–1885, p. 72). Since a terminal perianth is very common in liverworts, it seems likely that Spruce was highlighting the exposure of the perianth at the tip because of the lack of bracts or bracteoles, rather than its position.

Acromastigum A. Evans 1900—*akros* (at the tip, end) + *mastix* (flagellum or whip), “alluding to the flagella and their place of origin” (Evans, 1900, p. 103). The flagella arise from the postical segment of apical cells, rather than from the medulla as in *Bazzania*.

Adelanthus Mitt. 1864—*adeles* (uncertain) + *anthos* (flower), indicating the initial confusion about the nature of the perianth. “This species...has been long misunderstood from

- Dr. Taylor's mistake in considering the perianths to belong to some *Aneura* accidentally intermixed with the original specimens.... The discovery of the perianths on Mr. Spruce's specimens has at last set to rest the hitherto doubtful place of this species." (Mitten, 1864, p. 243). Müller (1912–1916, p. 206) attributed the name, not quite correctly, to uncertainty about the origins of the male and female organs.
- Allisoniella* E. A. Hodgs. 1965—after Kenneth Willway Allison (1894–1976), New Zealand forester and bryologist (Hodgson, 1965, p. 80). Among many contributions to bryology, Allison coauthored with John Child two classic books on New Zealand bryophytes, *The Mosses of New Zealand* and *The Liverworts of New Zealand* (Allison & Child, 1971, 1975). Hodgson must have known that the name *Allisonia* had already been applied in bryology by Herzog.
- Anastrophyllum* (Spruce) Steph. 1893—*anastrophe* (a backward turn) + *phyllon* (leaf), alluding to the strong bending of the leaves to the dorsal side of the stem. Spruce invented the name in 1876 for a subgenus of *Jungermannia*: "This group...is remarkable for the way the somewhat rigid, rufous leaves turn upwards" (Spruce, 1876, p. 234).
- Andrewsianthus* R. M. Schust. 1961—after Albert LeRoy Andrews (1878–1961), widely respected American philologist and bryologist at Cornell University, + *anthos* (flower). Andrews was Honorary Curator of the Wiegand Herbarium at the university. He was well known for his contributions on the Sphagnaceae and Bryaceae, but published on many other moss groups and also on liverworts (Steere, 1962).
- Aneura* Dumort. 1822—*an-* (lacking) + *neuron* (nerve), alluding to the lack of a midrib in the thallus: "Frons ecostata" (Dumortier, 1831, p. 85).
- Anthoceros* L. 1753—*anthos* (flower) + *keras* (horn), from the hornlike sporophyte. The name was coined in 1729 by Micheli (see *Bazzania*), who apparently thought that the sporophyte was the male inflorescence (Müller, 1912–1916, p. 589).
- Aphanolejeunea* A. Evans 1911—*aphanes* (invisible) + *Lejeunea*, "in allusion to the inconspicuous character of the species" (Evans, 1911, p. 273) and the original placement of the type species in *Lejeunea*.
- Archilejeunea* (Spruce) Schiffn. 1893—*archi-*, combining form of *archos* (chief) or *arche* (primal, original) + *Lejeunea*. Spruce's intention is not clear, but I think the name probably alludes to his note that the plants are large when compared to other species then included in *Lejeunea* (Spruce, 1884–1885, p. 88).
- Asterella* P. Beauv. 1805—diminutive of Latin *astrum* (star), referring to the starlike shape of the archegoniophores when seen from above.
- Austrofossombronia* R. M. Schust. 1994—Latin *auster* (the south) + *Fossombronia*, reflecting the largely far southern distribution of the genus and its close alliance to *Fossombronia*, from which it was separated.
- Austrolejeunea* (R. M. Schust.) R. M. Schust. 1963—Latin *auster* (the south) + *Lejeunea*. The name was first established by Schuster as a subgenus of *Siphonolejeunea* to accommodate *Siphonolejeunea olgae*, a southern temperate species then known only from New Zealand.
- Austroscyphus* R. M. Schust. 1985—Latin *auster* (the south) + *skyphos* (cup), alluding to the southern distribution of the genus and its original placement in *Neesioscyphus*.
- Bazzania* Gray 1821—after Matteo Bazzani (1674–1749), professor of anatomy at the University and Academy of Sciences at Bologna, first secretary of the Academy and of the Institute of Science, and patron of the celebrated Italian botanist Pier Antonio Micheli. Samuel Gray named numerous other genera after patrons and friends of Micheli; see Hawksworth's notes in the facsimile reprint of Micheli's *Nova Plantarum Genera* (Micheli, 1729).
- Balantiopsis* Mitt. 1867—*balantion* (a purse) + *opsis* (appearance), presumably from the purselike appearance of the leaf produced by the large dorsal lobe. (Not after Benedict "Benjamin" Balansa [1825–1891], French botanist and explorer.)
- Blepharidophyllum* Ångstr. 1873—*blepharis* (eyelash) + *phyllon* (leaf), alluding to the very ciliate leaves.
- Brevianthus* J. J. Engel & R. M. Schust. 1981—*brevis* (short) + *anthos* (flower), alluding to the very short branches on which the androecia and gynoecia occur.
- Calypogeia* Raddi 1818—*kalyx* (flower or fruit covering) + *hypogaea* (underground), referring to the buried marsupium. Raddi took the name from *Jungermannia calypogeia*, a synonym of the type species *Calypogeia fissa*.
- Calypetrocolea* R. M. Schust. 1967—*kalyptra* (covering, veil) + *koleos* (sheath), alluding to the large bracts that surround and hide the unfertilized gynoecium.

- Caudalejeunea* (Steph.) Schiffn. 1895—Latin *cauda* (tail) + *Lejeunea*. According to Gradstein (1994), so named for its caudiform gemmiparous shoots, which are characteristic of this genus.
- Cephalomitron* R. M. Schust. 1995—a combination of *Cephalozia* and *Gymnomitron*, alluding to the earlier placement of the only species, *Cephalomitron aterrimum*, in *Cephalozia* (and *Cephaloziella*) and its similarity to *Gymnomitron*, with which it was once grouped in the family Gymnomitriaceae.
- Cephaloziella* (Spruce) Schiffn. 1893—diminutive of *Cephalozia*, alluding to the size of the single species *Cephaloziella pygmaea* on which Spruce based a subgenus of *Cephalozia* “Plantae pusillae minutave” (Spruce, 1884–1885, p. 399). The name *Cephalozia* is apparently derived from *kephale* (head, end) + *ozos* (bud), referring to the headlike shape formed by the enlarged bracts and bracteoles (Müller, 1912–1916, p. 8).
- Ceratolejeunea* (Spruce) Schiffn. 1893—*keratos* (horned) + *Lejeunea*, alluding to the hornlike extensions of the keels of the perianth: “Perianthia superne 4–5 angula, angulis apice in cornua erecta vel varie patula saepe praelonga protractis” (Spruce, 1884–1885, p. 77).
- Chaetophyllopsis* R. M. Schust. 1960—*chaite* (hair, bristle) + *phyllon* (leaf) + *opsis* (appearance), alluding to the leaves with “margins freely developing long, setose cilia formed of single cells” (Schuster, 1960, p. 70).
- Chandonanthus* Mitt. 1867—*chandon* (with mouth wide open, yawning) + *anthos* (flower), alluding to the wide mouth of the perianth of the type species, *Chandonanthus squarrosus* (Menzies ex Hook.) Mitt. Müller (1951–1954, p. 619) suggested that the name was not appropriate for European species.
- Cheilolejeunea* (Spruce) Schiffn. 1893—*cheilos* (lip, edge) + *Lejeunea*. “The name of the group refers to the fact that the perianth often becomes two-lipped upon the extrusion of the capsule at maturity, a condition brought about by rupture and therefore of but slight taxonomic importance.” (Evans, 1906); “...carinis posticis humilibus obsoletisve saepe in unam latam fere confluentibus, demum ore bilabiata” (Spruce, 1884–1885, p. 79).
- Chiloscyphus* Corda 1829—*cheilos* (lip, edge) + *kyphos* (bent), alluding presumably to the shape of the mouth of the perianth. The name was first published by August Corda (see *Preissia*) in 1829 as *Cheilocyphos*. Dumortier (1831, p. 67) considered this name to be contrary to the rules of nomenclature and corrected it to *Chiloscyphus*. Unfortunately this obscured Corda’s original etymology, so that later authors assumed the root of the second part to be *skyphos* (cup). Grolle (1970) successfully argued for conserving Dumortier’s spelling because of its general usage since 1831 and its use in forming the names of other genera such as *Heteroscyphus* and *Notoscyphus*.
- Chonecolea* Grolle 1957—*chon* (funnel) + *koleos* (sheath), alluding to the shape of the perianth.
- Clandarium* (Grolle) R. M. Schust. 1984—presumably based on the Latin *clandestinus* (secret, hidden) but altered to avoid an illegitimate tautonym in the name of the type species. The name was coined by Grolle (1965) as a subgenus of *Blepharidophyllum* with *Clandarium clandestinum* as the type.
- Clasmatocolea* Spruce 1885—*klasmatos* (fragmented) + *koleos* (sheath), alluding to the perianth, which “is so fragile that the slightest touch breaks off the short unequal lobes at the wide mouth” (Spruce, 1884–1885, p. 440).
- Cololejeunea* (Spruce) Schiffn. 1893—*kolos* (with parts missing, maimed) + *Lejeunea*, alluding to the lack of underleaves: “Foliola nulla” (Spruce, 1884–1885, p. 79). Müller (1912–1916, p. 667) gave the same etymology.
- Colura* (Dumort.) Dumort. 1835—*kolouros* (dock-tailed), a compound of *kolos* (cut off, stump-horned) and *oura* (tail), alluding to the appearance of the perianth of the type species, *Colura calyptrifolia*, in which each of the five keels ends in a triangular process resembling a docked tail. Dumortier first used the name for a section of *Lejeunea* that he later raised to generic rank. Müller (1912–1916, p. 678) related the etymology to the same perianth feature, but mistakenly gave the prefix root as *koleos* (sword sheath). Dumortier’s name is perhaps a clever double entendre, as the shape of the leaves of *C. calyptrifolia* resembles a loaded weaving spindle or distaff—*colura* in Latin.
- Conoscyphus* Mitt. 1873—*konos* (cone) + *skyphos* (cup), presumably alluding to the shape of the perianth. (But see *Chiloscyphus*.)
- Cryptochila* R. M. Schust. 1963—*kryptos* (hidden) + *-chila* (from *Plagiochila*), apparently alluding to the group’s doubtful position in the Plagiochilaceae (Schuster, 1963, p. 284).

- Cuspidatula* Steph. 1901—Latin *cuspidatus* (tapering to a rigid point), alluding to the characteristic shape of the leaves.
- Cyanolophocolea* R. M. Schust. 2001—*kyanos* (dark blue) + *Lophocolea*, alluding to the blue oil bodies and the original placement of the type species (*Cyanolophocolea echinella*) in *Lophocolea*, a name that reflects the crested perianth (*lophos* crest + *koleos* sheath).
- Cyathodium* Kunze 1834—*kyathos* (ladle or cup) + *-odes* (similar to), i.e., similar to a cup, no doubt alluding to the shape of the gynoeceum (not the capsule, as suggested by Müller [1906–1911, p. 234]).
- Dendroceros* Lindenb. & Nees 1846—*dendron* (tree) + *keros* (horn), alluding to the habitat (the bark of trees) with the addition of the usual hornwort suffix.
- Dendrolejeunea* (Spruce) Lacout. 1908—*dendron* (tree) + *Lejeunea*, alluding to the dendroid growth habit of the one species (*Dendrolejeunea fruticosa*) and its original placement in *Lejeunea*.
- Dendromastigophora* R. M. Schust. 1987—*dendron* (tree) + genus *Mastigophora*, the first part presumably alluding to the habitat rather than the habit. *Dendromastigophora flagellifera* ranks with *Hepatostolonophora paucistipula* as the longest extant binomial in Australasian bryology.
- Diplasiolejeunea* (Spruce) Schiffn. 1893—*diplassio* (double) + *Lejeunea*, “from the two-ranked stipules” (Spruce, 1884–1885, p. 73).
- Diplophyllum* (Dumort.) Dumort. 1835—*diploos* (folded) + *phyllon* (leaf), alluding to the folding of the leaf to form a dorsal lobe.
- Drepanolejeunea* (Spruce) Schiffn. 1893—*drepanon* (sickle) + *Lejeunea*, alluding to the shape of the underleaves, which have a pair of narrow, widely spreading and curved lobes which together form a distinct sickle shape (Müller, 1912–1916, p. 647).
- Drucella* E. A. Hodgs. 1962—after Helen and Tony Druce, “whose collections of hepatics have been most valuable” (Hodgson, 1962, p. 47). Helen Druce is the daughter of Amy Hodgson and is an active member the Wellington Botanical Society. Her husband Tony (1920–1999) was a highly respected botanist with the New Zealand Department of Scientific Industrial Research.
- Dumortiera* Nees 1824—after Bethélemy Dumortier (1797–1878), Belgian botanist and bryologist, an early champion of the classification of plants into natural orders. Fifteen extant Australian liverwort genera were named by him.
- Enigmella* G. A. M. Scott & K.G. Beckmann—diminutive of Latin *aenigma* (a riddle), reflecting the puzzling morphology of the only species, *Enigmella thallina* (K. Beckmann, pers. comm., 2007).
- Eotrichocolea* R. M. Schust. 1963—*eos* (dawn, early) + *Trichocolea*, alluding to Schuster’s view that the genus represents an ancient lineage (Schuster, 2000).
- Fossombronia* Raddi 1818—after Conte Vittorio Fossombroni (1754–1844), minister to the Grand Dukes Pietro Leopoldo and Ferdinand III, distinguished for his efforts to improve the agriculture of Tuscany by drainage and irrigation.
- Frullania* Raddi 1818—after Leonardo Frullani (d. 1841), Florentine Privy Counselor and director of the Tuscan Treasury (Müller, 1912–1916; Stotler, 1968) and a colleague of Fossombroni.
- Gackstroemia* Trevis. 1877—Trevisan named the genus originally as *Gackströmia* but gave no etymology. It is presumably based on a person’s name, perhaps a variant of the Swedish surname Backström. The type species (*Gackstroemia magellanica* = *Jungermannia magellanica* Lamarck) was collected by Commerson in the Straits of Magellan, so the name does not refer to the collector.
- Geocalyx* Nees 1833—*gaea* (earth) + *kalyx* (fruit or flower cover), alluding to the buried marsupium.
- Goebelobryum* Grolle 1962—after Karl Ritter von Goebel (1855–1932), professor of botany at the University of Munich, noted for his work on plant morphology. He traveled in Australia and New Zealand in 1898, collecting the type of *Goebelobryum grossitextum* in Western Australia and a specimen of *Goebelobryum unguiculatum* in New South Wales (Grolle, 1962).
- Gongylanthus* Nees 1836—*gongyle* (carrot or other root vegetable) + *anthos* (flower), alluding to the long marsupium that grows down into the soil after fertilization (Müller, 1906–1911, p. 504).
- Gymnomitrium* Corda 1829—*gymnos* (naked) + *mitrium* (cap), alluding to the lack of a perianth.
- Haplomitrium* Nees 1833—*haploos* (simple) + *mitrium* (cap), alluding to the translucent sheath covering the developing capsule.

- Harpalejeunea* (Spruce) Schiffn. 1893—*harpa* (harp) + *Lejeunea*, referring to the bifid underleaves that have a shape resembling an ancient Greek harp. Spruce named several of his subgenera of *Lejeunea* for the shape of the underleaves (e.g., *Drepanolejeunea*).
- Hepatostolonophora* J. J. Engel & R. M. Schust. 1979—*hepatikos* (liver) + *stolon* (root) + *phoros* (bearing), i.e., a liverwort with stolons, which are profuse. The name replaced *Stolonophora*, which was already in use for an algal genus when Engel and Schuster published *Stolonophora* in 1975 (Engel & Schuster, 1979, p. 91).
- Herbertus* Gray 1821—according to Evans (1917) and Little (1949), after George Herbert, a patron of Micheli (see under *Bazzania*). Claimed by Ammons (1940) to be after English botanist William Herbert (1778–1847), for which the vascular genus *Herbertia* was named, but that is inconsistent with Samuel Gray's other names. Gray published this name twice in his *Systematic Arrangement of British Plants*, based on different types. In his list of corrections in the same volume he changed the second to *Pallavicinia* (Gray, 1821, p. 775).
- Herzogobryum* Grolle 1964—after Theodor Herzog (1880–1961), German bryologist in Jena, who worked largely on tropical liverworts. Herzog had coined the name *Chondrophyllum* for the genus, but that name was already in use (Schuster, 1996, p. 20).
- Heteroscyphus* Schiffn. 1910—*heteros* (different) + *skyphos* (cup), alluding to the difference in the position of the androecia (“lateraliter ex angulis amphigastriorum ortes”) and in the shape of the perigonal leaves compared to the stem leaves (“caulinis omnino dissimilibus”)—the features Schiffner felt warranted the separation from *Chiloscyphus*, in which the androecia were “intercalaria in caule primario et ramis aequalibus” and the perigonal leaves were “caeterum foliis caulinis omnino aequalibus” (Schiffner, 1910, p. 170, 171). See also *Chiloscyphus*.
- Hygrolembidium* R. M. Schust. 1963—*hygros* (wet, moist) + *Lembidium*, alluding to the habitat (wet soil) of the type (*Hygrolembidium isodictyon* = *Hygrolembidium acrocladum*) and its original placement in the genus *Lembidium* (Schuster, 1963, p. 277). “*Lembidium*” is a variant of Latin *limbium* (small border), probably alluding to the patch of hyaline cells in the leaf base.
- Hymenophyton* Dumort. 1835—*hymenos* (membranaceous) + *phyton* (plant), presumably alluding to the thin wings of the lobes of the thallus, although in his diagnosis Dumortier (1835, p. 25) described only the sporophyte.
- Isolembidium* R. M. Schust. 1968—*isos* (equal) + *Lembidium*, alluding to the isophylly of the type species *Isolembidium cucullatum* and its original placement in the genus *Lembidium* (Schuster, 1963, p. 278).
- Isophyllaria* E. A. Hodgs. & Allison 1965—*isos* (equal) + *phyllon* (leaf), alluding to the subequal leaves and underleaves of the type species, *Isophyllaria murrayana* (Hodgson, 1965, p. 68).
- Isotachis* Mitt. 1854—*isos* (equal) + *taxis* (arrangement), alluding to the regular arrangement of the \pm equal leaves and underleaves; “Folii incuba, amphigastriaque fere conformia” (Mitten, in Hooker, 1854, p. 148).
- Jackiella* Schiffn. 1900—after Joseph Bernhard Jack (1818–1901), pharmacist, botanist, and bryologist in Salem, Germany: “Genus hoc distinctissimum sincero animo dicavi amicissimo Dri J. B. Jack, seniori hepaticologorum praeclero” (Schiffner, 1900, p. 114). Jack was highly respected by European bryologists, and his obituary in *Hedwigia* was written by Franz Stephani (Stephani, 1901).
- Jamesoniella* (Spruce) Carrington 1881—named by Richard Spruce (as a subgenus of *Jungermannia*) after the fern genus *Jamesonia*: “Those species are all so like miniature copies of *Jamesonia* among ferns...that I propose to form them into a subgenus, and call it *Jamesoniella*” (Spruce, 1876, p. 230). The fern genus *Jamesonia* was named in 1830 by William Hooker after William Jameson (1796–1873), Scottish physician and botanist in South America, who in Ecuador collected the type of *Jamesonia imbricata* Hook. & Grev., the type species (Hooker, 1864, p. 106). Mistakenly said by Ammons (1940) to be after James Jameson (1856–1882), “English” (actually Irish) naturalist, and by Koperski (1991) to be after Hampden Gurney Jameson (1852–1939), English botanist in Ecuador.
- Jensenia* Lindb. 1868—presumably after Thomas Jensen (1824–1877), teacher and bryologist in Ranum, Denmark. Lindberg coined the name to replace *Mittenia* Gottsche, a later homonym of *Mittenia* Lindberg.
- Jubula* Dumort. 1835—diminutive of Latin *iuba* (mane, crest, beard), alluding to the persistency of the elaters after capsule rupture, forming a

- “beard,” a feature common to all species (Müller, 1912–1916, p. 637). Curiously, *iuba* can also mean “helmet”; perhaps Dumortier realized the added appropriateness of the name because of the helmet-shaped ventral lobule of the leaf. The name *Jubula* is conserved against *Salviatus* Gray, an earlier but not accepted name.
- Jungermannia* L. 1753—after Ludwig Jungermann (1572–1653), physician and professor of anatomy and botany at Giessen and later at Altdorf (Nürnberg), a contemporary of Dillenius and Micheli (Levrault, 1822). *Jungermannia* is a pre-Linnaean name first published by Heinrich Rupp in 1718 in his *Flora Ienensis* (Rupp, 1718).
- Kurzia* G. Martens 1870—After Wilhelm Sulpiz Kurz (1834–1878), German botanist, specialist in bananas and bamboos and curator of the botanic gardens in Calcutta (now Kolkata).
- Leiomitra* Lindb. 1875—*leios* (smooth, flat, bald) + *mitron* (cap), alluding to the smooth, bractless calyptra. Lindberg created the genus to separate Gottsche’s section *Laevifolia* from *Trichocolea* (Engel, 1999, p. 25). This genus was found for the first time in Australia at Growling Swallet in Tasmania, during the Ninth Australasian Bryological Workshop in 2007.
- Lejeunea* Lib. 1820—after Alexandre Louis Simon Lejeune (1779–1858), French physician and botanist in Verviers, author of *Flora des Environs de Spa* (1811–1813) and, with R. J. Courtois, *Compendium Florae Belgicae* (1828–1836) (Müller, 1912–1916, p. 655). Belgian botanist Marie-Anne Libert of Malmédy sent her early collections of plants to Lejeune. Her original spelling was *Lejeunia*.
- Lepicolea* Dumort. 1835—*lepis* (scale) + *koleos* (sheath), alluding to the leaflike outgrowths on the perianth: “Colésule recouverte d’écailles semblables aux feuilles” (Dumortier, 1835, p. 20). Dumortier seems to have preferred the shorter form *Lepicolea* rather than *Lepidocolea* because it is more harmonious in Latin. Scott (1960, p. 129) noted that Dumortier preferred *Tricholea* over *Trichocolea* for the same reason.
- Lepidolaena* Dumort. 1835—*lepidos* (scaly) + *laena* (mantle, cloak), alluding to the scaly perianth: “Colésule recouverte d’écailles imbriquées et foliacées...” (Dumortier, 1835, p. 13).
- Lepidolejeunea* R. M. Schust. 1963—*lepidos* (scaly) + *Lejeunea*. The etymology is uncertain.
- Lepidozia* (Dumort.) Dumort. 1835—*lepis* (scale) + *ozos* (bud), alluding to the scalelike bracts and bracteoles surrounding the perianth: “Perichaetium polyphyllum, phyllis squamiformibus indivisis.” (Dumortier, 1831, p. 69). Dumortier applied the name first to a section of *Pleuroschisma*, a defunct genus that included species now in *Bazzania* and other modern genera.
- Leptolejeunea* (Spruce) Schiffn. 1893—*leptos* (thin, slender) + *Lejeunea*, alluding to the slender plants: “Pusillae tenui strato” (Spruce, 1884–1885, p. 76).
- Leptophyllopsis* R. M. Schust. 1963—*leptos* (thin, slender) + *phyllon* (leaf) + *opsis* (appearance), an appropriate name for this monotypic genus: “with...leaves that are characteristically glistering, very delicate and large-celled (cells... very leptodermous)” (Schuster, 1963, p. 270).
- Leptoscyphus* Mitt. 1851—*leptos* (thin, slender) + *skyphos* (cup), presumably alluding to the flattened perianth, which resembles that of *Radula* species. Müller (1906–1911, p. 781) was, I think, wrong in translating *leptos* as “klein” (small, little).
- Lethocolea* Mitt. 1867—*lethe* (missing, overlooked) + *koleos* (sheath), alluding to the marsupium, which is usually so deeply buried in the soil that it is torn off when the plant is collected, or simply overlooked.
- Leucolejeunea* A. Evans 1907—*leukon* (white) + *Lejeunea*, alluding to the pale color of the plants.
- Lopholejeunea* (Spruce) Schiffn. 1893—*lophos* (crest) + *Lejeunea*, alluding to the lacinate keels of the perianth: “Per. compressa 4-carinata, carinis late alato-cristatis” (Spruce, 1884–1885, p. 74). The name is conserved against Stephani’s *Lopho-Lejeunea*.
- Lophozia* (Dumort.) Dumort. 1835—*lophos* (crest) + *ozos* (bud), alluding to the typically dentate mouth of the perianth: “contractée et dentée au sommet” (Dumortier, 1835, p. 17).
- Lunularia* Adans. 1763—Latin *lunula* (little moon), alluding to the crescentic gemma cups on the dorsal surface. The name was first used by Micheli in 1729. Linnaeus (1753) included the only species, *Lunularia cruciata*, in *Marchantia*.
- Marchantia* L. 1753—after Nicolas Marchant (d. 1678), director of horticulture at the Jardin du Roi and a favorite of Gaston Duc d’Orléans. The genus was originally named in his honor in 1713 by his son Jean Marchant (1650–1738),

- who also became director of horticulture at the Jardin du Roi (Hus, 1911).
- Marsupella* Dumort. 1822—diminutive of Latin *marsupium* (money bag, pouch), alluding to the appearance of the perianth that, in some species, encloses the developing capsule.
- Marsupidium* Mitt. 1867—as for *Marsupella*.
- Mastigolejeunea* (Spruce) Schiffn. 1893—*mastix* (flagellum, whip) + *Lejeunea*, alluding to the common occurrence of flagellate branches: “alii (pauci) flagellares parvifolii decurvi radicantes” (Spruce, 1884–1885, p. 100).
- Mastigophora* Nees 1838—*mastix* (flagellum, whip) + *phoros* (bearing), alluding to the flagellate branches.
- Megaceros* Campb. 1907—*megas* (giant) + *keras* (horn): “The name is selected on account of the very large size of the sporophyte in the commonest Javanese species. This in some instances reaches a length of 9 cm and possibly more...” (Campbell, 1907, p. 469).
- Metalejeunea* Grolle 1995—*meta* (changed) + *Lejeunea*, alluding to the previous positioning of the type species (*Metalejeunea cucullata*) by various authors in *Lejeunea*, *Acrolejeunea*, *Eulejeunea*, and *Microlejeunea*.
- Metzgeria* Raddi 1818 — A name honouring Johann Metzger (1771–1844), German copper engraver and art restorer from Staufen, Breisgau (Baden-Württemberg), a friend of Raddi and pupil of the great Florentine engraver Raphael Sanzio Morghen (1753–1833): ‘Metzgeria nome da me consacrato all’amicizia del valentissimo Incisore in rame e restauratore di Quadri antichi Sig. Giovanni Metzger di Stauffen in Brisgovia, allievo del celebre Sig. Raffaello Morghen.’ (Raddi 1818: 46). Metzger became an important art agent in Florence (Danz 2003: 45–46) and, in about 1828, acquired artworks by David Ghirlandaio now owned by the Metropolitan Museum of Modern Art in New York. Koperski (1991) wrongly aligned the name with Johann Christian Metzger (1789–1852), landscape architect and director of the botanic gardens in Heidelberg.
- Microlejeunea* (Spruce) Steph. 1890—*mikros* (small) + *Lejeunea*, alluding to the small size of the plants. Spruce coined the name for a subgenus of *Lejeunea* in 1884.
- Mnioloma* Herzog 1930—*mnion* (moss) + *loma* (edge, border), alluding to the border of hyaline cells on the leaf, typical of the genus. The genus was first reported from Australia by Renner (2006).
- Monocarpus* D. J. Carr 1956—Latin *mono* (one) + Greek *karpos* (fruit), presumably suggesting a monocarpic (i.e., annual) nature. Proskauer (1961) created the new and clever name *Carrpos* for the genus on the assumption that *Monocarpus* D. J. Carr was a later homonym of *Monocarpus* Post & Kuntze. Unfortunately his name was not validly published, and *Carrpos* now stands as a lonely synonym of *Monocarpus* D. J. Carr.
- Neogrollea* E. A. Hodgs. 1965—Latin *neo* (new) + *Grollea*, named in honor of bryologist Riclef Grolle (1934–2004) who spent much of his career studying austral liverworts. Hodgson must have been aware that the name *Grollea* had been published by Schuster in 1964 for a genus of liverworts.
- Nothogymnomitrium* R. M. Schust. 1996—*nothos* (false) + *Gymnomitrium*, alluding to its closer similarity to *Gymnomitrium* than to *Herzogobryum*, from which it was separated by Schuster (Schuster, 1996, p. 45).
- Notoscyphus* Mitt. 1873—*notos* (south) + *skyphos* (a cup), a puzzling name, presumably alluding to a southerly distribution of the type species *Notoscyphus lutescens* (although then known from both north and south of the equator) and its resemblance to a *Chiloscyphus* (although placed in family Jungermanniaceae).
- Otolejeunea* Grolle & Tixier 1980—*oto*, combining form of *ous* (ear) + *Lejeunea*, undoubtedly alluding to the pair of lobes on the perianth, having a remarkable resemblance to the ears of Mickey Mouse.
- Pachyschistochila* R. M. Schust. & J. J. Engel 1982—*pachys* (thick) + *Schistochila*, alluding to “the marked and almost universal tendency for the leaves to become polystratose” (Schuster & Engel, 1982, p. 177).
- Pallavicinia* Gray 1821—according to Ammons (1940) and Koperski (1991), named after Lazarus Pallavicini, Italian botanist and archbishop of Genoa. However, it might equally be named after Italian naturalist Ignazio Alessandro Pallavicini, or after the Marquis Adalberto Pallavicini delle Frabose, first president of the Societa Agraria in Turin. The name was ignored for 40 years until its priority was noted by Carruthers (1865, p. 302).
- Paracromastigum* Fulford & J. Taylor 1961—*para* (next to, near) + *Acromastigum*, alluding to the presence of *Acromastigum*-type ventral branching, one of the characters that separates it from *Lepidozia* (Fulford & Taylor, 1961, p. 336).

Paraschistochila R. M. Schust. 1963—*para* (next to, near) + *Schistochila*, reflecting the close relationship between the two genera.

Pedinophyllum (Lindb.) Lindb. 1874—*pedinos* (flat) + *phyllon* (a leaf), reflecting the flatness of the leaves when compared to those of *Plagiochila*, from which the type species (*Pedinophyllum interruptum*) was separated (Müller, 1906–1911, p. 775).

Petalophyllum Nees & Gottsche ex Lehm. 1844—*petalon* (petal, lamellum) + *phyllon* (leaf), alluding to the lamellate lobes of the thallus.

Phaeoceros Prosk. 1951—*phaios* (dusky, greyish brown) + *keros* (horn), the second part alluding to the hornwort group and the first part alluding to the typical color of the mature sporangium: “*Phaeoceros* because of the usual colour of the mature sporangium.” (Proskauer, 1951, p. 347). Strangely, this color is neither a primary nor a secondary characteristic of the genus as defined by Proskauer.

Plagiochasma Lehm. & Lindenb. 1832—*plagios* (oblique, slanting) + *chasma* (cleft, chasm), alluding to the fissures in the side of the carpocephalon in which the archegonia lie.

Plagiochila (Dumort.) Dumort. 1835—*plagios* (sideways, slanting) + *cheilos* (lip, edge), alluding to the oblique mouth of the perianth: “Colésule comprimée par les flancs, fendue d’un côté...” (Dumortier, 1835, p. 14). Dumortier coined the name originally for a section of *Radula*, later raising it to generic rank. Müller (1906–1911, p. 759) strangely interpreted *cheilos* here to mean “perianth”; compare with *Chiloscyphus*. Perhaps he recognized that the word always applied to the perianth mouth and so merely took a linguistic shortcut.

Plagiochilion S. Hatt. 1947—as for *Plagiochila*.

Pleurozia Dumort. 1835—*pleura* (rib) + *ozos* (bud), presumably alluding to the pleated fertile perianths, contrasting with the smooth, tubular sterile perianths (“tubi vacui”): “Colésule...denticulee et plissée au sommet” (Dumortier, 1835, p. 15). Müller (1912–1916, p. 526), interpreting *pleura* to mean “side,” attributed the name to the lateral position of the gynoecia, which seems very doubtful as this was not mentioned by Dumortier.

Plicanthus R. M. Schust. 2002—Latin *plica* (fold) + *anthos* (flower), alluding to the strongly plicate perianth.

Podomitrium Mitt. 1855—*pous* (foot) + *mitrion* (cap), alluding to the specialized fertile branches developed on the ventral side of the thallus.

Porella L. 1753—diminutive of Latin, *porus* (pore). The name was coined by Dillenius in his *Historia Muscorum* of 1741, believing the plant to be a moss with capsules in which the spores were released through pores in the side (Ammons, 1940; Swails, 1970). Linnaeus likewise classified it as a moss. Scottish nurseryman and botanist James Dickson, a founding member of the Linnean Society whose name is remembered in the tree-fern genus *Dicksonia*, was the first to recognize that *Porella* was a liverwort (Swails, 1970).

Preissia Corda 1829—after Balthazar Preiss (1765–1850), physician and botanist in Prague (Koperski, 1991). August Karl Corda (1809–1849) was a botanist, mycologist, and zoologist at the Prague Museum.

Pseudocephalozia R. M. Schust. 1965—*pseudēs* (false) + *Cephalozia*, presumably alluding to the similarity in habit to that genus.

Psiloclada Mitt. 1854—*psilos* (naked, unarmed) + *klados* (branch or shoot), alluding to the absence of flagella, which Mitten considered separated the only species *Psiloclada clandestina* from *Lepidozia* (Mitten, in Hooker, 1854, p. 143).

Ptychanthus Nees 1838—*ptychos* (folded or pleated) + *anthos* (flower), in reference to the deeply and multiply pleated (keeled) perianth.

Pycnolejeunea (Spruce) Schiffn. 1893—*pyknos* (dense, thick) + *Lejeunea*, presumably alluding to the appearance of the plants, which Evans (1906, p. 21) noted have closely overlapping leaves and often form pure mats.

Radula Dumort. 1822—Latin *radula*, a scraper, universally understood to refer to the flattened and truncate perianth, very much like a scraper for removing paint.

Reboulia Raddi 1818—after Eugene de Reboul (1781–1851), Italian botanist in Florence (Müller, 1906–1911, p. 255; Little, 1949, p. 8). Quattrocchi (2000) stated that the name honors the French naturalist Henri Paul Irénée Reboul (1763–1839), but this seems unlikely, as he was principally a mineralogist. Raddi’s original spelling, *Rebouillia* (later also *Reboullia* and *Reboulea*), was corrected by Nees von Esenbeck in 1846 (Little, 1949, p. 8).

Rectolejeunea A. Evans 1906—Latin *rectus* (fragile) + *Lejeunea*, “in allusion to the fact that the leaves in most of the species easily become broken off” (Evans, 1906, p. 9).

Riccardia Gray 1821—most likely after Octavius Riccardi of Florence, who paid for the printing of Micheli’s *Novum Plantarum Genera*

- (Koperski, 1991). Claimed by Ammons (1940) to be after Francesco Ricciardi (1758–1842), Conte di Camaldoni, but this is very unlikely considering the origins of Samuel Gray's other names and the different spelling. The name was originally published by Gray as *Riccardius* but was corrected to *Riccardia*, as proposed by Little (1949, p. 21).
- Riccia* L. 1753—after Pietro Francesco Ricci or Ricco, Italian botanist and politician in Florence. The name was coined by Micheli in 1729 (Spruce, 1884–1885, p. 570).
- Ricciocarpos* Corda 1829—*Riccia* + *karpos* (fruit), alluding to the sporophytes, which resemble those of *Riccia*.
- Riella* Mont. 1852—after Michel-Charles Durieu de Maisonneuve (1796–1878), French soldier and botanist. Montagne, stymied by Mérat's prior use of the name *Durieu* for a genus of flowering plants, chose this diminutive form based on "Du Rieu." Proskauer (1965, p. 503) noted that all the synonymous names for this genus—*Duriaea* Bory & Mont., *Durieu* Mont., *Duriella* Bory ex Billot, *Duriena* Mont., and *Maisonneuvea* Trevis.—are named for the same person.
- Saccogynidium* Grolle 1961—*sakkos* (sack) + diminutive of *gyno-* (relating to the female organ), alluding to the marsupium.
- Scapania* (Dumort.) Dumort. 1835—*scapanion* (spade or hoe), alluding to the flattened, truncate perianth: "Colésule comprimée par le ventre et par le dos, tronquée au sommet." (Dumortier, 1835, p. 14). Dumortier originally published the name in 1831 for a section of *Radula* (Dumortier, 1831, p. 38).
- Schiffneriolejeunea* Verd. 1933—after Victor Schiffner (1862–1944), Bohemian-born Austrian botanist and bryologist, professor of botany at the University of Vienna. He worked at the Botanical Gardens in Buitenzorg (Bogor), treated the liverworts in Engler and Prantl's *Natürliche Pflanzenfamilien* (1893), and described many tropical Asian hepatics.
- Schistochila* Dumort. 1835—*schistos* (divided) + *cheilos* (lip), alluding to the lacinate mouth of the perianth: "Colésule...laciniée, à segments pinnatifido-dentés." (Dumortier, 1835, p. 15).
- Seppeltia* Grolle 1986—after Rodney David Seppelt (b. 1945), Australian bryologist in Hobart, noted for his work in Antarctica and the subantarctic, who collected the type on Macquarie Island.
- Siphonolejeunea* Herzog 1942—*siphon* (tube) + *Lejeunea*, a reference to the tubelike lobule. (See also *Austrolejeunea*.)
- Solenostoma* Mitt. 1865—*solen* (pipe) + *stoma* (mouth), referring simply to the shape of the perianth mouth. The name is conserved against Corda's name *Gymnoscyphus* (1835). Müller (1956–1958) strangely gave the etymology of the prefix as *Solen* (a marine mussel, commonly called a razor-shell), a name that in any case means "pipe."
- Sphaerocarpos* Boehm. 1760—*sphaira* (sphere) + *karpos* (fruit), alluding to the spherelike inflated involucre enclosing the capsules. The name was coined by Micheli in 1729.
- Spruceanthus* Verd. 1934—after Richard Spruce (1817–1893), English botanist and explorer in South America, author of the monumental *Hepaticae of the Amazon and the Andes of Peru and Ecuador* (Spruce, 1884–1885).
- Stenolejeunea* R. M. Schust. 1963—*stenos* (narrow) + *Lejeunea*, alluding to the narrow stem in comparison to *Taxilejeunea*, from which it was segregated (Schuster, 2000, p. 152).
- Stictolejeunea* (Spruce) Schiffn. 1893—*stictos* (spotted) + *Lejeunea*, alluding to the ocelli that give the plant a spotted appearance: "Sticto-Lejeunea, from the dotted leaves" (Spruce, 1884–1885, p. 73).
- Symphyogyna* Nees & Mont. 1836—*symphysis* (joining together) + *gyne* (female), presumably alluding to the tendency of the capsule segments to remain joined at the apex after the capsule has split.
- Targionia* L. 1753—A name coined by Micheli in honour of Florentine physician Cyprian Targioni (?fl. 1720s) for his contribution to the knowledge of herbal medicines (Micheli 1729: 3). Not, as is often claimed, after Italian physician and botanist Giovanni Targioni-Tozzetti (1712–1783), pupil of Pier Micheli and later curator of the botanical garden and professor of botany at the University of Florence, who would have been only 16 or 17 years old when Micheli published the name.
- Telaranea* Spruce ex Schiffn. 1893—Latin *tela* (web) + *aranea* (spider or spider's web), "alluding to the delicate cobweb-like appearance of the plants" (Engel & Smith-Merrill, 2002).
- Temnoma* Mitt. 1867—*temnos* (to cut) and perhaps *loma* (edge, border), an allusion to the lacerated appearance of the leaves. It is not unusual for authors to add or remove letters from the roots to make the name more harmonious (see, for example, *Trichocolea*).

Thysananthus Lindenb. 1844—*thysanos* (tasselled or tufted) + *anthos* (flower), alluding to the tassellike appearance of the perianth caused by the lacerated margins of the bracts.

Treubia K. I. Goebel 1890—after Melchior Treub (1851–1910), Dutch botanist and director of the Department of Agriculture at Buitenzorg, Dutch East Indies (Bogor, Indonesia), a contemporary of Karl von Goebel (see *Goebelobryum*). Treub offered hospitality and working facilities to Goebel and many other German and Austrian botanists who went to Buitenzorg to study the tropical Asiatic flora.

Triandrophyllum Fulford & Hatcher 1962—*triandros* (divided into three) + *phyllon* (leaf), alluding to the commonly trifid leaves.

Trichocolea Dumort. 1822—*trichos* (hairy) + *koleos* (sheath), alluding to the hairy perianth: “Colésule...entièrement couverte de poils.” (Dumortier, 1835, p. 20). Dumortier first published the name as *Tricholea* and subsequently as *Tricholea*, *Thricolea*, and *Tricolea*, before settling on *Tricholea*, noting that this contraction was preferable because the “correct” name *Trichocolea* was contrary to the spirit and harmony of the Latin language (Dumortier, 1835, p. 20). Nees von Esenbeck (1838), however, corrected the name to *Trichocolea* in 1838, and most subsequent authors followed his lead. Little (1949, p. 10–11) successfully argued for the conservation of *Trichocolea* against Dumortier’s other names.

Trichotemnoma R. M. Schust. 1968—*trichos* (hairy) + *Temnoma*, alluding to the very hairy appearance of the leaves compared to those of *Temnoma*.

Tuyamaella S. Hatt. 1951—after the celebrated Japanese botanist Takasi Tuyama (b. 1910), who collected the type species, *Tuyamaella serratifolia* (Hattori, 1947, p. 3). Hattori originally published the name without description in 1947. He no doubt chose the name in the knowledge that *Tuyamaea* had already been used for a genus of flowering plants.

Tylimanthus Mitt. 1867—the etymology of the prefix is uncertain. Mitten presumably based the name on *tylos* (a knob or swelling) + *anthos* (flower), alluding to the marsupium. The “m” might have been added to make the name more harmonious.

Vandiemenia Hewson 1982—“After Anthony Van Diemen of the Dutch East India Company, after whom Van Diemen’s Land (Tasmania) was first named by Abel Tasman in 1642.”

(Hewson, 1982, p. 163). As Governor-General of the Dutch East Indies, Van Diemen (1593–1645) was the principal force behind Tasman’s search for the “Great South Land.” The name New Holland, the Latinized form of which appears so often in botanical nomenclature, was coined by Tasman.

Wettsteinia Schiffn. 1898—after Richard Wettstein (1863–1931), Austrian botanist, professor of botany at the University of Prague and later the University of Vienna, a colleague of Victor Schiffner.

Zoopsis (Hook. f. & Taylor) Hook.f. ex Gottsche 1846—*zoon* (living being, animal) + *opsis* (appearance), presumably alluding to a fancied resemblance to a velvetworm or some other tiny invertebrate.

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